Para el Dr. E. J. Wellhausen
con todo el respeto y la
estimación del autor.

Angel Kato Y

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CYTOLOGICAL STUDIES OF MAIZE [ZEA MAYS L.] AND TEOSINTE [ZEA MEXICANA (SCHRÄDER) KUNTZE] IN RELATION TO THEIR ORIGIN AND EVOLUTION.

A Dissertation Presented

By

TAKEO ANGEL KATO YAMAKAKE

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Cytological Studies of Maize [_Zea_ _mays_ L.] and Teosinte [_Zea_ _Mexicana_ (Schrader) Kuntze] in Relation to their Origin and Evolution. [May 1975]

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ABSTRACT

Previous extensive analysis of chromosome knob distributions in maize suggested that similar studies in both teosinte and maize might provide further insights into their origin and evolution.

A comparative study of teosinte and maize pachytene chromosome morphology was undertaken from three different aspects: 1] the basic characteristics of length, arm ratio, chromomere distribution and knob position and size; 2] the knob frequency distribution in teosinte collections from its whole distribution range in Mexico and Guatemala, and maize collections from central Mexico; and 3] the presence of small inversions in teosinte chromosomes from different regions.

The length of corresponding teosinte and maize chromosomes is variable, but no differences exist at the species level. However, length differences may exist among races. The arm ratio and chromomere distribution are similar in both genomes. Various knob types may or may not be found at each of many fixed positions on the chromosomes. More knobbed positions were found in teosinte than in maize chromosomes. Mexican teosinte having mostly intercalary knobs is more similar to maize than Guatemalan teosinte, possessing only terminal knobs. These results confirm and substantiate

other studies that both species possess the same basic genome. Consequently, all existing teosintes are derivatives of a common ancestor and maize must have originated from a Mexican type of teosinte population complex.

Knobs at different positions on the chromosomes of teosinte and maize populations are not distributed at random, but populations having various unique knob combinations are found at the regional or racial level. In many cases, these knob combinations are sharply distinct in the races from adjacent regions. In some chromosomes, or chromosome arms possessing more than one knob position, their knobs tend to appear in different regions or races. These results indicate that: 1] the several knob types at different positions possess various adaptive values, so that different selection pressures can act upon them bringing about the non-random distribution observed; 2] knobs at different positions on the same chromosome have either or both compensatory or complementary effects; and 3] no evidence exists of a knob shifting mechanism in teosinte and maize chromosomes, so the existing populations are derivatives from a common ancestral population complex which had all of the knobs known at present.

Many knobs that exist in high frequencies in teosinte are absent in sympatric and hybridizing maize populations. Some of these knobs, however, are present in high frequencies in maize from regions where no teosinte exists at present. These facts indicate that at least the segments carrying these knobs do not introgress from teosinte into maize, strengthening the idea that knobs have different adaptive values.

Several inversions already reported in the literature and two new ones, causing a low frequency of pollen abortion, were found in teosinte

plants. The same inversions are present in widely separated populations without any geographical connection between them, a fact that supports further the idea that all teosintes were derived from a common population complex.

The known naturally occurring inversions in teosinte and maize populations are knobless or small knobbed, and usually located at or near known knob positions. Therefore, they might have different adaptive values and be knob substitutes for accomplishing the same role in evolution.

Based on the fact that knobs reduce the recombination rate in the segments carrying them, the possibility is proposed and discussed that knobs favor the development of supergenes, acquiring in this way various adaptive values.

That the process of genetic drift is not adequate for explaining all the results obtained in the present studies is also discussed.

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FIGURES 30 to 39. Geographical distribution of the relative frequencies of the several knob sizes [large, medium, small and knobless] found at different knob positions in collections of Guatemalan teosinte.

In each figure, the maps illustrate the distribution of: A. large knobs; B. medium knobs; C. small knobs; and D. knobless. Each circle represents a single collection. Black circles represent high frequencies [more than 2/3 of the total number of chromosomes of each collection]; half circles represent intermediate frequencies [1/3 to 2/3 of the total chromosomes]; open circles represent low frequencies [less than 1/3 of the total chromosomes]; and the X's represent absence of the particular knob condition that the specific map is considering.

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CHAPTER I

INTRODUCTION

General Antecedents

At present the origin of both maize and teosinte is still controversial. There are now two main currents of thinking prevailing in this respect. One theory considers that modern maize is a domesticated descendant of a now extinct wild maize which was also a progenitor of teosinte [Mangelsdorf, 1974]. The second theory, on the contrary, postulates that teosinte is the wild ancestor from which modern maize originated during domestication [Galinat, 1971, 1974a; Iltis, 1961; deWet and Harlan, 1972; Beadle, 1972]. At any rate both theories accept that among the members of the Maydeae teosinte is the closest relative of maize. Although many cytological considerations have been given for reaching the conclusion on the close relationship between maize and teosinte, the main foundations of both theories on the origin of these plant species are largely based on morphological grounds [Galinat, 1971, 1974a; Beadle, 1972; Mangelsdorf, 1974].

Chromosome knobs are heterochromatic structures of variable size found at fixed positions on the chromosomes of Zea, Tripsacum, and other members of the Gramineae. These structures of maize have been used in diverse ways, as chromosomal markers in cytogenetic studies of chromosomal aberrations, in investigations regarding the association between knobs and morphological and physiological characters, in the form of average numbers have been used in studies of racial characterization and relationships, etc. However, these studies have not contributed much toward the clarification of the problem concerning the origin and evolutionary relationships of maize and teosinte.

The preliminary studies of McClintock [1959, 1960] on chromosome knob constitutions and their geographical distribution in several selected races of maize in Latin America suggested that the knobs did not occur at random but they followed specific distribution patterns and she recommended an extensive study of the American races of maize. This task was first undertaken by Longley and Kato [1965] but unfortunately the data obtained were analyzed in terms of average knob numbers instead of knob positions. Recently, more extensive studies on chromosome morphology of maize populations from all over the Americas have resulted in the main conclusion that present maize populations are the result of admixtures of different original maize germplasms. These germplasms came from several localities by independent domestication from the wild ancestor which in turn was probably already differentiated into several distinct racial types [Kato and Blumenschein, 1967; McClintock, Blumenschein and Kato, unpublished].

So far, the chromosome morphology studies on teosinte are still limited and incomplete [Longley, 1937; Ting, 1958a, 1964]. This has been especially due to the fact that extensive collections from populations of different geographical regions have not been made until recently [Wilkes, 1967, 1972b].

With these antecedents in mind, it has been thought that the collection of chromosome knob data from teosinte populations on a larger scale eventually could lead into more insights into the problem of the origin and further evolution of maize and teosinte. Therefore an investigation has been undertaken of the chromosome morphology of maize and teosinte with the following objectives.

Objectives

1. To obtain further knowledge on the chromosome morphology of maize populations from regions where teosinte is also growing.

2. To obtain information on the chromosome morphology of teosinte populations from all the regions where it grows in the wild.

3. To make a comparative study of teosinte and maize with the information gathered in points 1 and 2. As a result, new insights may be gained on the problem of the origin and further evolutionary relationships between maize and teosinte populations.

Significance

The main purpose of this research is to shed light on the problem of the origin and evolution of maize and teosinte, the closest relatives among the members of the Maydeae. The importance of clarifying the origin of these plants resides not only in the academic value, but also in the fact that this is basic in understanding the genetic mechanisms that were responsible in transforming one species into the other. The more that is understood about the genetic mechanisms, the greater the opportunity to manipulate intelligently these plant species for man's benefit.

It is well known that maize is one of the world's most important food plants. Although genetic variability in maize is still available in many countries and this is being used in breeding new superior varieties of maize, the breeder eventually will have to look to its relatives for new kinds of genetic variability to solve specific problems or for trying new ways of improving maize varieties. Logically, he will find the use of the closest relative, teosinte, most promising. Here is where the knowledge gained on the genetic mechanisms that operated during the divergence and continued separation of the two species will find practical application. The more knowledge that is available when it is needed, the faster man can solve his problems.

CHAPTER II

REVIEW OF LITERATURE

Morphology and Taxonomy

General morphology. The general descriptive morphology of the maize and teosinte is now universally accepted without any objections. However, there have been differences in opinion about the morphological and taxonomic relationships in maize and its relatives.

The general morphology of maize has been described in much detail by Arber [1934], Anderson [1944a], Anderson and Brown [1948], Anderson and Cutler [1942], Bonnett [1948, 1953, 1954], Cutler and Cutler [1948], Kiesselbach [1949], Sass [1955], Weatherwax [1916, 1917, 1918, 1935 and 1955], and others.

The stalk consists of a series of nodes separated by internodes of varying lengths. Each node bears a leaf, which consists of a sheath and a blade. The leaves at successive nodes usually have an alternate and distichous arrangement. Each leaf subtends an axillary bud enclosed in a prophyll. The axillary buds located at the lower end of the main stem may develop into tillers or lateral vegetative branches with a morphological structure similar to that of the main axis. On the other hand, the buds borne at upper nodes have short internodes and modified sheaths, the husks, that enclose a terminal female or pistillate inflorescence [the ear]. The main axis is terminated by the male or staminate inflorescence [the tassel].

The male inflorescence usually is formed by a central axis and several spreading lateral branches, which may have secondary and tertiary branches. On this basic framework the inflorescence is organized into spikelets which are arranged in pairs, one member being sessile and the other pedicellate. The upper portion of the central axis, the central spike, shows a polystichous arrangement of the pairs of spikelets, while the lateral branches usually have a distichous arrangement. Each spikelet consists of two functional male florets all enclosed in two empty or sterile glumes. Each of the two florets of a spikelet is enclosed by two floral bracts, the lemma and the palea, enclosing three stamens, two lodicules and a rudiment of a pistil.

The female inflorescence, commonly called the ear, consists of pistillate spikelets borne in pairs forming many longitudinal rows on a thick axis, commonly called the cob of the ear. Each row of paired spikelets usually forms only two rows of kernels [caryopses] in the mature ear. This is so because only the upper flower of each spikelet is usually functional, the other remaining suppressed. The rachilla elongates to elevate the kernel above the empty glumes. The kernel enlarges and, thereby, emerges from its lemma and palea. Both pistillate spikelets may appear to be sessile because the pedicels may be short and fused into the cupule floor. The pistil of the female flower consists of a fused tricarpelar ovary, two of the carpels giving rise to two long styles or 'silks' which fuse except at the tip. The ovary contains a single campilotropous ovule with two integuments. Rudimentary stamens are present.

The vegetative morphology of the teosinte plant has been found to be basically similar to that described for the maize plant [Mangelsdorf, 1974; Mangelsdorf and Reeves, 1939; Weatherwax 1935, 1955; Wilkes, 1967.] The main differences between teosinte and maize are found in the inflorescences, especially the female inflorescences. The male inflorescence of teosinte has the same basic structure as that of maize with the exception that the former plant does not have a polystichously arranged central spike. While it is claimed by Wilkes [1967] that the Guatemalan teosintes do not possess a central spike in their tassels, one appears to be present in this teosinte when grown in our cultures at Waltham, Mass. The Mexican teosintes show conspicuous central spikes, and contrary to the maize central spike, always have a distichous arrangement of their spikelet pairs. The female inflorescences consist of two rows of single pistillate spikelets borne in alternately arranged cupulate rachis segments. Each female spike is enclosed in a husk. In each cupule only a single spikelet develops to maturity, the other spikelet of the pair remains as a "microscopic rudiment" on one side of the fruit case [Weatherwax, 1918, 1935, 1955].

A quantitative variation of different morphological traits in maize has been given in a series of publications describing the hundreds of races of maize found in Latin America [Wellhausen _et al._ 1952, 1958; Roberts _et al._ 1957; Hatheway, 1957; Brieger _et al._ 1958; Brown, 1960, Ramirez _et al._ 1960; Grobman _et al._ 1961; Timothy _et al._ 1961, 1963; and Grant _et al._ 1963]. Similar information for the races of teosinte has been given by Wilkes [1967].

Homology and origin of the inflorescences. The central spike of the tassel and ear of maize, having a polystichous arrangement of the spikelet pairs, uniquely deviate from the basic distichous structural pattern of the Gramineae. This situation was realized by Wigand as early as 1854 and since that time the finding of an explanation to the problem of the origin of the maize inflorescences, but especially the female inflorescence or the ear, has been the central subject of the more general theme about the origin of the maize plant [Galinat, 1956, 1959, 1963, 1967, 1970, 1971, 1974a; Mangelsdorf, 1945, 1959, 1965, 1974; Mangelsdorf and Reeves, 1939; Weatherwax, 1918, 1935, 1955].

Two aspects have been of importance in the study of the tassel and ear of maize: the homology between the two types of inflorescences and the phylogenetic mechanism for their origin.

That both structures of the inflorescences of maize are homologous to each other has been clearly pointed out in early investigations [Weatherwax, 1935] or in other words as Mangelsdorf [1945] stated "since the appearance of Montgomery's paper [in 1906] the homology of the ear with the central spike of the tassel has not been seriously challenged except, perhaps, by indirection".

Further investigations have provided definitive evidence about the tassel-ear homology and also that this homology is valid between maize and its closest relatives, teosinte and Tripsacum.

That distichy and polystichy are expressed in segregates of maize-teosinte hybrids showing a high correlation between the central spike of the tassel and the ear has been found by Langham [1940].

Clear evidences showing correlations between tassel internode condensation and increase in row number in the ear, tassel branch length and ear length, tassel branch pattern and ear shape, and tertiary branches and irregular rowing in the ear, have been found by Anderson [1944a]. Further studies of Anderson and Brown [1948] on the row numbers in the tassel as well as in the ear, have shown that the homology between the two inflorescences, with respect to this character, is basically very simple [the row numbers in the ear are correlated with the number of spikelet pairs per whorl in the tassel] and that in those cases where this correspondence is obscure, the cause is found in the action of the phenomenon of condensation or telescoping of successive internodes.

In the progeny of the cross between Guarani maize from Paraguay and a pod corn, Mangelsdorf [1945] has found plants bearing long and stretched ears, some of them with basal branches resembling the tassels. The main difference was that instead of having staminate spikelets, they had pistillate spikelets. He concluded that "there is now no doubt, if there was doubt before, that the ear is the homologue of the central spike of the tassel".

By studying the vascular organization of the central spike of the tassel and the cob of the ear of maize, Laubengayer [1949] and Reeves [1950, 1953] suggested the now obsolete idea that both organs possess two separate vascular systems, one inside the other, and both forming a cylindrical "hollowed" network. Galinat [1959] has shown that the two apparent vascular systems actually are connected in the glume cushions. The innermost vascular bundles are large and supply mainly the spikelets. The outer bundles are small and supply chiefly the rind of the rachis and the outer glume of the spikelets. One of the differences between the vascular system in the central spike of the tassel and that in the cob resides in the amount of central pith tissue surrounded by the larger bundles.

Another approach toward the demonstration of the homology between the tassel and the ear of maize and its relatives has been those studies regarding the internal anatomy and development of the prophyll and the cupule, and applying the concept of the phytomer, the basic structural unit of the plants. Galinat [1956, 1959, 1970] concluded that, to the traditional definition of the phytomer as composed by an internode, a leaf and an axillary bud, should be added a fourth component, the prophyll, and that this component is developed as the cupule or its lining tissue in the ear, as the pulvinus in the axils of the tassel branches, the palea in the staminate and pistillate flowers and the prophylls proper in the axils of lateral branches in the tillers and the lateral ear bearing shoots [shanks].

Through detailed developmental investigations of the vegetative and floral primordia of maize, Bonnett [1948, 1953, 1954] has also established the tassel-ear homology, since he has found that the early stages of the development of the two types of inflorescences essentially do not differ in the component elements formed and the origin and further growth of the primordia of these components. Furthermore, he concluded that any dissimilarity in the morphology of the mature tassel and ear is the product of the differences in action patterns of the later stages of the developmental controlling systems. This conclusion seems to be further supported by the common observation that in the tillers of normal maize, and under certain genetic or environmental conditions, portions or the whole tassel of the main stalk can develop pistillate spikelets and the ear can develop staminate segments or anthers intermixed with pistillate spikelets [Bonnett, 1948; Cutler and Cutler, 1948; Mangelsdorf, 1945, 1974; Mangelsdorf and Reeves, 1939; Reeves, 1950, 1953; Weatherwax, 1918, 1935, 1955].

Although the above mentioned studies have definitely established the homology between the tassel and the ear, this homology does not give any explanation about the origin of the inflorescences of maize as such.

Therefore, parallel to the studies regarding tassel-ear homology, several hypotheses on the probable origin of these inflorescences, especially of the ear, have been proposed [Galinat, 1963, 1967, 1970, 1974a; Mangelsdorf, 1945, 1948, 1974; Mangelsdorf and Reeves, 1939; Weatherwax, 1918, 1935, 1955].

The early hypotheses have been reviewed by Weatherwax [1918, 1935], Mangelsdorf [1945] and Mangelsdorf and Reeves [1939]. These are three: [1] the fusion hypothesis; [2] hypothesis of the twisting of a two-ranked spike, and [3] the hypothesis of the contraction or reduction of branches.

1. The fusion hypothesis was first proposed by Hackel [1890] and regards the ear of maize as formed by double rows of kernels, each row corresponding to a single spike of teosinte.

The appearance of branched ears with some frequency in populations of maize has been one of the major evidences supporting this hypotheis. However, it is impossible to obtain ears with ten, fourteen, or eighteen rows if these are the result of the fusion of distichous spikes, since each of the latter would contribute four rows. Therefore, the fusion theory presents "mathematical inconsistencies" as concluded by Weatherwax [1918, 1935].

When a variety of maize from the Guarani Indians of Paraguay is crossed to pod corn and backcrossed to Guarani maize, the progeny plants produced very elongated and stretched ears with the terminal portions resembling the central spike of the tassel. In some cases these ears possessed basal branches. Mangelsdorf [1945] studying these ears interpreted them as ears corresponding to an association between a central spike and upper lateral branches of the tassel. He concluded that this evidence completely invalidates the fusion hypothesis.

Frequently central spikes of tassels bear segments with an ear-like structure. Since the staminate and the pistillate portions are on different parts of the same axis, there would be difficulty to explain this fact by accepting the fusion theory [Reeves, 1950, 1953]. Also Reeves [1953] by studying branched ears and stems and assuming that "the maize plant with tillers has the same relation to the plant without tillers as the ear with monopodial branches has to the unbranched ear", concluded that the branched ears "are no better evidence for fusion in the ear than branched culms are for fusion in the culm".

2. The second hypothesis was advanced by Collins [1919] after his studies of pistillate spikes of an F_2 progeny of a maize x teosinte hybrid. In these spikes he found a series of transitional forms between the teosinte spike with the typical ear of maize. The steps are: a] the suppressed pistillate spikelet becomes functional; b] the axis of the rachis segments shorten and become more numerous and crowded; c] adjacent rachis segments are positioned at the same plane and unite or become "yoked" in pairs; and d] the axis of the spike twists so that the "yoked" rachis segments become perpendicular from each other forming a four-rowed ear and further twisting of the axis will form ears with higher ranking. His main evidence of "yoking" in the ear of maize was that the dropping of rows always occurred on opposite sides of the ear and not from two adjacent rows.

This hypothesis has been objected mainly by Weatherwax [1935] who found no evidence of "yoking" of spikelet pairs on opposite sides of the rachis in the ears of maize. He showed that the dropping of rows is always by pairs of adjacent rows and not by two rows from opposite sides of the rachis as stated by Collins [1919]. Also Mangelsdorf [1945] stated that probably the yoking has not occurred in the origin of the maize ear simply because the spikelets on opposite sides of the rachis behave differently from each other.

3. The hypothesis of the reduction of branches was first advanced by Collins [1912] who proposed that the ear of maize originally was a panicle, the branches of which were shortened until each of them were represented only by a pair of spikelets. Descriptions of the ramosa mutant in maize by Weatherwax [1918] has given further support to this hypothesis. However, Weatherwax [1935] indicated that this hypothesis explains satisfactorily the origin of spikelet pairs, but still fails in explaining the origin of polystichy of the ear of maize. He proposes, then, an alternate interpretation based on the theory of spiral phyllotaxy. However, Mangelsdorf [1945] objects to this interpretation because it is only descriptive and not explanatory of the distichous and polystichous conditions. Anderson [1944] further modified the concept of branch reduction of Collins by suggesting that a whorl of spikelets resulted from the condensation of the secondary branches down onto the primary axis.

In his studies of the South American Guarani maize crossed with pod corn as mentioned above, Mangelsdorf [1945] concluded that in all cases the ears of maize represent compact inflorescences, indicating that in the origin of the ear this characteristic, compaction or shortening of internodes, has been very important.

Reeves [1950, 1953] by showing a series of tassels with different degrees of branch reduction, interpreted them as representing the probable steps of the ear evolution from a paniculate type of inflorescence. Based on these observations he supported the idea that the "unbranched ear of maize is the immediate result of the condensation of a panicle with many polystichously arranged branches". He also concluded that the origin of the polystichy had in its first stages a decrease in length and later elimination of internodes.

The condensation index or the average number of spikelet pairs per apparent node was devised by Anderson [1944a]. By using this index in correlation studies between tassel condensation and row number of the ear, Anderson and Brown [1948] concluded that the tassel is "fundamentally distichous throughout" with the upper part or central spike having branches reduced to whorls of paired spikelets and with an intermediate portion of the tassel with partially reduced branches. This tassel organization has been interpreted by them as the result of a gradual action, from base to tip of the tassel, of the phenomenon of condensation or telescoping of successive internodes. This process also operates in the same way in the ear and those varieties of maize with very compact ears have accumulated several modifier genes during domestication which permitted condensation of the ear without fasciation.

Once the importance of the concept of compaction, condensation or telescoping of internodes in the evolutionary development of the inflorescences of maize was realized and well established, the hypothesis of the reduction of branches became modified in its basic proposition of a lateral reduction of branches by a concept of vertical reduction of the axis and the way was opened toward a better understanding of the evolutionary steps for the development of the tassel and the ear of present maize. Also a new concept is introduced into the hypothesis, the differential action of several sets of genetic factors on similar primordia for developing morphologically different but homologous organs.

In a series of studies regarding the comparative developmental morphology of floral parts of maize and its relatives and using the phytomer concept, Galinat [1956, 1957, 1959, 1963, 1969, 1970, 1971, and 1974a] has been able to develop an explanation of the most probable evolutionary steps by which the ear of modern maize was originated under domestication from its wild ancestor, teosinte; the basic sequence of his developments are as follows:

1. The cupulate rachis segment has evolved in several ways in different genera and species, in some cases as a structural devise for protecting the caryopses and in other cases only as a structural support for the caryopses. This evolution of the cupule is seen "in a graded series of species starting with the Andropogoneae and terminating with the American Maydeae" [Galinat, 1956].

2. The morphological organization of maize and its relatives is better understood as a structure composed of a fundamental set of organs, the phytomer, which can be variously developed through the action of different genetic factors in the different species and also in space and time within a given species, but always maintaining their respective homology [Galinat, 1957, 1963, 1969].

3. In the domestication of maize from its wild ancestor, it could have been selected during the accumulation of genes affecting condensation and differentiation of the staminate and pistillate inflorescences. In

this way a plant type with a very compact, unbranched, many rowed ear covered by husks and a less compact, flexible and branched tassel, could have originated [Galinat, 1969, 1970, 1971, 1974a].

4. The ears as found in modern maize have been evolved from an ancestral spike like that of present teosinte. This conclusion has been reached by a comparative study of the cupule morphology of modern teosinte, maize and their hybrid progeny and also of archaeological maize remains. It was shown that in this material a series of cupule shapes are found intergrading between two extremes, teosinte and modern maize, which represent a part of the postulated evolutionary sequence [Galinat, 1970, 1971, 1974a].

Taxonomy. Maize, Zea mays L., and teosinte Zea mexicana [Schräder] Kuntze and Zea perennis [Hitchcock] Reeves and Mangelsdorf, together with the genus Tripsacum, form the American Maydeae of the family Gramineae. The other members of this tribe, Coix, Polytoca, Chionacne, Trilobachne, and Schlerachne, are all Asiatic [Hackel, 1890; Hitchcock, 1922, 1930, 1951; Reeves and Mangelsdorf, 1942; Wilkes, 1967; Mangelsdorf, 1974].

The name of maize, Zea mays L., has been maintained unchanged since Linneus described and named it in 1753. Teosinte, which was described by Schräder in 1832 for the first time under the name of Euchlaena mexicana, contrary to maize has had several names since different authors, by describing different specimens introduced into Europe from Mexico and Guatemala, have given different botanical names [e.g. Reana giovanninii Brignolia; Reana luxurians Durien; Reana angustifolia Durien; Euchlaena luxurians Durien et Ascherson; Euchlaena bourgaei Fournier]. Furthermore, during the botanical history of maize and teosinte, both were placed under different tribes of the grass family [e.g. Zeineae, Paniceae, Phalarideae, Olyrearum, Maydeae] sometimes both in the same tribe, and in other cases in different tribes and even more the differently named teosintes were placed under different tribes [Hitchcock, 1922, 1930; Reeves and Mangelsdorf, 1942]; Wilkes, 1967].

The most stable and unifying taxonomic treatment of the maize and teosinte plants ~~has~~ been that given by Hackel [1890] in his monograph of the Gramineae. He placed Zea mays L. and Euchlaena mexicana Schräder along with the other American genus Tripsacum and four Asiatic genera, Coix, Chionachne, Schlerachne, and Polytoca, in the tribe Maydeae. This tribe was distinguished from the Andropogoneae by being monoecious.

In 1904, Otto Kuntze, through the works of Watson in 1891 and of Harshberger in 1896, became aware of the fact that maize and teosinte easily produce hybrids and he made Zea and Euchlaena congeneric. Therefore, the genus Zea being monotypic before became bitypic with Zea mays L. for maize and Zea mexicana [Schräder] Kuntze for teosinte [Wilkes,1967].

Later, in 1910, Hitchcock collected a type of perennial teosinte in Ciudad Guzman, in the state of Jalisco in Mexico, and described it as a new species given the name Euchlaena perennis Hitchcock. This teosinte type was collected again in 1921 by Collins in the same locality confirming Hitchcock's discovery [Hitchcock, 1922].

Unaware of the taxonomic change made by Kuntze, and based on similar arguments, Reeves and Mangelsdorf [1942] reached the same conclusion and made the change of Euchlaena into Zea, such that maize and teosinte are congeneric. However, as Wilkes [1967] states, Kuntze has priority over the change of generic name of annual teosintes but not of the perennial one, so the names should read, Zea mexicana [Schräder] Kuntze for the annual and _Zea perennis_ [Hitchcock] Reeves and Mangelsdorf for the perennial form. The generic change for teosinte has become widely accepted [Celarier, 1957; deWet, _et al_., 1971; Galinat, 1959; Iltis, 1969; Rollins, 1953; Shaver, 1962; Sinnott, Dunn and Dobzhansky, 1958; Stebbins, 1950].

Darlington [1963] stated that there are breeding and cytological evidences which suggest that maize and teosinte could be placed under the same species, but he still maintains both names, _Euchlaena mexicana_ and _Zea mays_.

More recently, Iltis [1972], following Darlington's suggestion, has proposed a formal taxonomic change within the genus _Zea_. He considers only two species, _Z. mays_ L. and _Z. perennis_ [Hitchcock] Reeves and Mangelsdorf. The former species includes three subspecies, ssp. _mays_, for cultivated maize, ssp. _mexicana_ for annual Mexican teosinte and ssp. _luxurians_ for annual Guatemalan teosinte.

Chromosome Numbers in _Zea_

The determination of the basic chromosome number of maize began with the pioneer studies of Kuwada [1911, 1915, 1919, 1925] and later investigations of Longley [1924, 1925, 1927], Kiesselbach and Petersen [1925], Fisk [1925, 1927], Reeves [1925], Randolph and McClintock [1926] and Randolph [1928a]. The chromosome number of teosinte was studied by Kuwada [1915, 1919], Longley [1924], and Kiesselbach and Petersen [1925].

That the basic chromosome number of maize and teosinte is x=10 was realized since almost the beginning of these series of investigations. In his first observations, Kuwada [1911, 1915] found that the haploid chromosome numbers in maize varieties varied from 9 to 12, and suggested that the basic number was 12 and that varieties with this original number gave origin to varieties with lower numbers. Further observations, however, led Kuwada [1919] to conclude that the basic number is 10.

Although the poorly developed cytological techniques of that time were a factor for causing some difficulties, the major problem that the investigators met was that several varieties have consistently shown plants having chromosome numbers higher than the basic number of 10, a problem that was puzzling for almost two decades. Diverse mechanisms were proposed as explanations to account for the presence of extra chromosomes: 1] segmentation of individual chromosomes was proposed by Kuwada [1919] and considered by Fisk [1925, 1927]; 2] fusion of chromosomes in contrast to segmentation was also advanced by Kuwada [1919]; 3] Kiesselbach and Petersen [1925] thought that some kind of mutation was responsible for the origin of the variation rather than irregularities in chromosome behavior during mitosis; 4] duplication through non-disjunction or asynapsis and random segregation of chromosomes were advanced by Fisk [1927], an explanation also accepted by Randolph [1928a] who also considered another possibility for the origin of the extra chromosomes through hybridization of diploid plants with a triploid or another polyploid condition. All these explanations were based on the assumption that the extra chromosomes had their origin in the chromosomes of the normal complement. Although Randolph [1928a] observed that the extra chromosomes behaved independently and irregularly with respect to the chromosomes of the normal complement regarding pairing and segregation, the studies of Longley [1927], Randolph, [1928b] and McClintock [1933] have shown that these extra chromosomes do not belong to any of the normal chromosomes or part of them, but they are chromosome types having completely different morphology and behavior.

Even though much knowledge has been gained on the cytological behavior and genetic effect of the B chromosomes, their origin is still unknown.

Chromosome Morphology

General chromosome morphology. During the investigations for establishing the basic chromosome numbers for maize and teosinte, there has been an emphasis in finding ways to distinguish the different chromosomes of the complement. McClintock [1929] was the first to demonstrate that the 10 chromosomes of maize can be identified cytologically through her observations on chromosomes of the first mitosis of the microspore. In the same article McClintock [1929] mentions for the first time the presence of knobs on different chromosomes.

Later McClintock [1930, 1932] extended these observations to the prophase of meiosis where she found that the pachytene stage was more adequate for chromosome studies because of their elongation revealing many of the detailed morphological features of each chromosome, such as, relative lengths of the chromosomes, precise location of the centromere determining the relative length of the arms, characteristic positions of the knobs and certain conspicuous chromomeres. In her detailed studies on the pairing process of homologous and non-homologous chromosomes and chromosome segments, McClintock [1933] published the first complete idiogram of the pachytene chromosomes of maize. She reported 11 knob positions distributed in 9 of the 10 chromosomes in different genetic stocks of maize. In these studies, McClintock [1933] observed pachytene chromosomes in maize monoploids, diploids, monosomics, trisomics, deficiencies, inversions, translocations, ring chromosomes, and "asynaptic" plants and was able to show evidence that association of pachytene chromosomes is always 2 by 2 between homologous or non-homologous segments. Although non-homologous associations appear as intimate as homologous ones, at diakinesis they tend to disappear.

In his studies of chromosome behavior of Florida teosinte, Beadle [1932] reported 11 terminal knobs in the mitotic karyotype.

In more extensive studies carried on later by Longley [1937, 1938, 1941], a similarity was shown in the basic morphology of the pachytene chromosomes of maize from different varieties of the North American Indians and regions of Mexico with those of teosinte from Mexico and Guatemala. He found that although the chromosome length varies depending upon the stage of contraction when measured and the arm ratio also may vary because of possible differential contraction rates of the two arms of each chromosome, the average length and arm ratio of the chromosomes of maize and teosinte are relatively constant. This similarity resides in actual length measurements but more precise comparisons have been observed when homologous chromosomes from different sources are brought together in the F_1 hybrids [Longley, 1939].

A detailed account of the characteristic features of each maize pachytene chromosome have been given by Longley [1938] and Rhoades [1955].

More recently, Maguire [1962], by having measured the 10 pachytene chromosomes from 271 microsporocytes of maize stocks representing the sixth and seventh backcross to maize of a maize and Tripsacum hybrid, found similar chromosome lengths and arm ratios and their variances as those reported by Longley [1939]. The statistical analysis of these data led

Maguire [1962] to conclude that there are two kinds of variability in the chromosomes, one is a factor that acts uniformly upon the whole genome and a second factor which may be specific for each chromosome but not related to the length. It is not known how much the length of the chromosomes and their arms at mid-pachytene is dependent upon genetic background or upon environmental conditions, or more probably to an interaction of both.

The total number of knob positions reported were 18 for maize, 21 for Mexican teosintes, and 18 for Guatemalan teosintes. Maize and Mexican teosintes are more similar regarding the knobs because most of them are intercalary, and both differ from the Guatemalan teosintes in that the latter possess all their knobs at the end of the chromosomes. However, 3 terminal knobs [e.g. 4S, 7S and 9S] are common in both maize and most teosinte and 6 terminal knobs [e.g. 3S, 4S, 5S, 7S, 8S and 9S] are found in both Guatemalan and Mexican teosintes [Longley, 1937, 1938, 1939, 1941]. At present the number of known knob positions in maize chromosomes is set at about 22 [Rhoades, 1955; Longley and Kato, 1965; Kato, 1961, 1964; Kato and Blumenschein, 1967; Bianchi, Ghatnekar, and Ghidoni, 1963; Ghatnekar, 1965]. The number of knob positions for Mexican teosintes has remained unchanged [Ting, 1964].

One of the chromosomes in maize and teosinte [chromosome 6] is always attached to the nucleolus, therefore, is the most easily identified chromosome of the complement. McClintock [1934] has conclusively shown that the knob-like structure in the short arm of chromosome 6 in maize is the nucleolar organizer. When this heterochromatic organizer is broken into two parts, each portion is capable of organizing a nucleolus. The attachment of the nucleolus to its organizer is variable in different strains.

It can be located at the distal end, at the middle region, or at the proximal end of the organizer [McClintock, 1934].

The appearance of pachytene chromosomes varies from strain to strain. In some the chromosomes are clumped, showing only a few free segments, while in others the spreading of the chromosomes is so good that each of them can be followed easily from end to end and, in most of the cases, an intermediate condition seems to prevail. Randolph [1948] and Wellwood and Randolph [1957], by crossing different maize inbred lines with distinct extreme pachytene conditions and observing cytologically the F_2 and backcross progenies, concluded that the clumped versus wellspread pachytene character does not follow a single Mendelian inheritance and that it probably is polygenic.

Abnormal chromosome 10. In some varieties of maize and of teosinte, an unusual chromosome 10 has been observed. Generally it is accepted that the first description of this chromosome 10 in maize was made by Longley [1938] who found it in some of the North American Indian maize strains. However, in a previous paper [Longley, 1937], he introduced this chromosome in his Figure 17 and described it as "abnormally long".

This abnormal chromosome 10 consists of an additional segment similar in length to the short arm, which is located at the end of the long arm of normal chromosome 10. This extra segment possesses a large knob subterminally located at its distal end. Another characteristic of the abnormal 10 is the usual presence of one or two large chromomeres near the junction of the extra segment with the normal long arm [Longley, 1938].

Longley [1937] also reported an abnormal chromosome 10 in plants of a teosinte strain that he received from Chapingo, Mexico. In general, it is similar to the abnormal chromosome 10 described for maize with the only difference that the extra segment carries a terminal knob in addition to the subterminal large knob.

The abnormal chromosome 10 is widely distributed among different races of maize from Latin American countries and from North American Indians [Longley, 1938; Longley and Kato, 1965; McClintock, Blumenschein and Kato, unpublished; Moreno and Grobman, 1960; Timothy, et al., 1963; McClintock, 1960].

It is of interest to note that the abnormal chromosome 10 has not been reported in any of the maize varieties studied from Europe and Asia [Anderson and Brown, 1953; Bianchi, Ghatnekar and Ghidoni, 1963, 1964; Ghatnekar, 1965; Lorenzoni, 1965; Suto, 1957, 1958, 1959, 1960; Suto and Yoshida, 1956; and Tavcar, 1957, 1961].

The inheritance of the abnormal chromosome 10 was studied by Rhoades [1942] showing that it is preferentially segregated during megasporogenesis when heterozygous with the normal chromosome 10. By using the r marker, he found that more than 70% of the megaspores received the abnormal 10 instead of the expected 50%.

That the abnormal chromosome 10 is segregated preferentially through the megaspores has been confirmed in subsequent studies [Rhoades, 1952; Rhoades and Dempsey, 1957, 1966; Longley, 1945; Emmerling, 1959; Kikudome, 1959].

Rhoades [1942, 1952] postulated that at least one crossing over must occur in the long arm during the first meiotic division. Then an equational segregation for the extra segment at anaphase I will produce a heteromorphic dyad that, during anaphase II, segregates preferentially the abnormal chromosome 10 to the functional basal megaspore.

Maize plants having the abnormal chromosome 10, either in homozygous or heterozygous condition, show an abnormal behavior in that secondary centric regions [neocentromeres] are formed in the chromosome arms in positions other than at the normal centromere [Rhoades and Vilkomerson, 1942].

When a chromosome pair of the complement other than chromosome 10 is heterozygous for a chromosome knob and also the abnormal chromosome 10 is present, the knobbed chromosome is segregated preferentially at megasporogenesis. This was discovered by Longley [1945] who obtained 64 percent of the functioning megaspores having _C_ allele when a plant heterozygous for the abnormal chromosome 10 and a knob _C_/knobless _c_ chromosome 9 pair was pollinated by a plant with normal chromosome 10 and a homozygous knobless _c_ chromosome 9. Similar results were obtained by Longley [1945] working with chromosome 6. Later studies have confirmed Longley's results [Kikudome, 1959; Emmerling, 1959] and further they demonstrated that the degree of preferential segregation depends upon the knob size; the larger the knob, the higher the rate of preferential segregation.

The number of neocentromeres formed is correlated with the number of knobs present in the cells. This finding led Rhoades [1952] to conclude that the neocentromeres are formed on the knobs and that they are the cause of the observed preferential segregation. In maize, the four megaspores are arranged linearly and only the basal one becomes functional, so that if a crossing over between the knob and centromere produces a heteromorphic dyad at the first division, and because the knobbed chromatid forms a neocentromere, it will reach first the pole in relation to the knobless chromatid, and if this orientation is maintained until the occurrence of anaphase II, then the preferential segregation of the knobbed chromosome is easily understood [Rhoades, 1952, 1955; Rhoades and Dempsey, 1966].

From the studies of preferential segregation, it was clear that the factor or factors causing it are located on the extra segment of the abnormal chromosome 10, but it was not clear precisely where they are located within the extra segment. This problem was somewhat clarified by Emmerling [1959] who by the comparison of two altered abnormal chromosomes 10 [e.g. K^o lacking completely the knob and the distal euchromatic segment and K^s lacking only a distal portion of the knob and the distal euchromatic segment] found for the K^o that the knob and the distal euchromatic segment have an important role in the expression of preferential segregation, but still somewhat contradictory results were found with the K^s, which she could not explain.

Although the discovery of the phenomenon of preferential segregation for abnormal chromosome 10 is interesting and important, it also has other more fascinating and far reaching effects. It has the ability to increase recombination as well as to interact with knobs changing the recombination rates in different ways for various segments, depending upon whether the knob is homozygous or heterozygous, the knob is large, small or is absent, and whether the segment is distal or proximal with respect to the knob [Rhoades and Dempsey, 1957, 1966; Kikudome, 1959].

In their studies with chromosome 3, Rhoades and Dempsey [1957, 1966] have shown that in homomorphic condition the recombination rate in the distal region _Lg2-A_ was constant whether the chromosome 3 was knobbed or not [the knob lies closely linked to _Lg2_ but distal to it] or whether the abnormal chromosome 10 was present or not, while the proximal region G16-Lg2 showed an increased recombination in the presence of the abnormal chromosome 10 and a decrease rate with the normal 10. The increase in recombination was highest in the presence of the knob and the abnormal 10. On the other hand, with a heteromorphic chromosome 3 [large knob-knobless condition] the Lg2-A region showed a reduction in the recombination rate with respect to the homomorphic case, with a higher reduction in the absence of the abnormal chromosome 10, and in the G16-Lg2 region, an increase in the rate of recombination. This increase was, again, higher in the presence of the abnormal chromosome 10.

The results of Kikudome [1959] working with the short arm of chromosome 9 were essentially the same to those of Rhoades and Dempsey [1957, 1966], that is, the recombination rate was increased in the presence of the abnormal chromosome 10. However, Kikudome [1959] obtained additional information since he found that, in the absence of the abnormal chromosome 10, the knobbed-knobless heterozygous chromosome 9 showed a negative correlation between the size of the knob and crossing over.

The origin of the abnormal chromosome 10 is still unknown. However, some years ago, Ting [1958b] proposed the hypothesis that the abnormal chromosome 10 originated by a "simple translocation" between a normal chromosome 10 and a B chromosome, based on morphological similarities of the extra segment of the abnormal chromosome 10 and certain portions of the B chromosomes. Three subsequent investigations have invalidated Ting's hypothesis. Kikudome [1961] working with Ting's abnormal chromosome 10 found that it did not undergo preferential segregation itself, and further, it did not induce this type of segregation in knobbed chromosome 9. More recently, Carlson [1969b]; by using the A-B translocation, TB-9b, was able to show that the abnormal chromosome 10 cannot substitute 9^B chromosome for the induction of nondisjunction of the B^9 chromosome, while it would be expected to do so if the extra segment of abnormal chromosome 10 had some homology with B chromosomes. The invalidity of Ting's hypothesis was also demonstrated by Snope [1967] who compared the meiosis of haploids having the abnormal chromosome 10 or the normal chromosome 10 and carrying a single B chromosome, finding that the number of bivalents in the two classes of haploids was similar, indicating that the extra segment of the abnormal chromosome 10 does not have any homologous portion with B chromosomes.

Emmerling [1958] has found that the abnormal chromosome 10 carry on nondisjunction when present in homozygous or heterozygous condition. She also found isochromosomes of the abnormal chromosome 10 and deficient duplicate type of translocations formed by adjacent-1 disjunction in heterozygous reciprocal translocations between the abnormal chromosome 10 and other chromosomes not identified. The occurrence of these aberrations was explained as the result of the neocentric activities in the knobs induced by the abnormal chromosome 10 which, in turn, can cause unusual segregations and breakage of the chromosomes.

B chromosome. The first to disclose the existence of supernumerary chromosomes was Longley [1927] who also studied the meiotic behavior of these chromosomes finding that their segregation during the first division of microsporogenesis is erratic. These chromosomes were called B chromosomes by Randolph [1928b] in order to differentiate them from the A chromosomes of the normal complement. The morphological description of the B chromosomes and their synaptic behavior at pachytene were given by McClintock [1933]. According to McClintock [1933], B chromosomes are about one-half the length of chromosome 10 and comprise several distinct morphological parts: 1] terminal centromere, 2] heterochromatic knob-like portion, 3] euchromatic region, which forms about one-third of the total length, 4] elongated heterochromatic segment with various constrictions, 5] bulky heterochromatic segment, and 6] a broken heterochromatic segment with four distinct parts. Later on it has been found that the centromere of the B chromosomes is not terminal, but there is a short arm composed of one or two chromomeres [Darlington and Upcott, 1941; Randolph, 1941; Ward, 1973b; Carlson, 1970]. However, this does not rule out that a truly terminal centromere in certain B chromosomes exists as one variant [Darlington and Upcott, 1941; Rhoades, 1955].

McClintock [1933] found that non-homologous pairing is frequent among these unusual chromosomes regardless of whether they occur in odd or in even numbers. Also she found that when there are more than two B chromosomes, they form multivalents similar to the A chromosomes. Pairing at any point along the chromosomes is always 2 by 2, and they never show association with any part of the A chromosomes.

The presence of B chromosomes among different maize types was known since the pioneering studies on the chromosome number of this plant started by Kuwada [1911, 1915, 1919, 1925], and others. Subsequent studies have shown that this chromosome type is widely distributed in maize varieties all over the world [Bianchi, Ghatnekar and Ghidoni, 1963; Brown and Anderson, 1947; Ghatnekar, 1965; Kato, 1964; Kato and Blumenschein, 1967; Longley, 1938; Longley and Kato, 1965; McClintock, 1959, 1960; McClintock, Blumenschein and Kato [unpublished]; Moreno and Grobman, 1960; Suto, 1957, 1958, 1959, 1960; Suto and Yoshida, 1956, Tavcar, 1957, 1961; Timothy, et al., 1961, 1963].

It is known from Longley [1937] and Wilkes [1967] that B chromosomes are also present in teosinte. B chromosomes have been reported in Tripsacum by Tantravahi [1968] and Chandravadana, Rao and Galinat [1970].

The first studies on the meiotic segregation and inheritance of the B chromosomes were made by Longley [1927] who, by crossing maize plants with 0, 1 and 2 B chromosomes, showed that these chromosomes undergo non-disjunction, and after analyzing his data under the assumption that this non-disjunction occurs at random during second meiotic division of both the megasporogenesis and microsporogenesis, he concluded that non-disjunction occurred at a more constant rate on the female side and was more variable on the male side, and also that differential death rate eliminate a portion of the megaspores with B chromosomes. Later Randolph [1941], by making crosses between plants with different numbers of B chromosomes and counting the chromosome numbers in the progeny, obtained results showing that when the male parent had B chromosomes, plants with higher and lower numbers of extra chromosomes than the expected ones appeared in the progeny. He found no irregular behavior of the chromosomes during microsporogenesis that could explain these results. He suggested that the responsible events could have occurred during the second mitosis of the microspore, but because of technical difficulties, he did not make direct observations. Randolph [1941] also failed to find evidence for the presence of any known A chromosome genes on the B chromosomes. However, by selecting for large numbers of B's per plant, he found that various deleterious effects, such as reduction in fertility, decreased vigor, defective seeds, etc., appeared. The effect of B chromosomes on pollen size in maize has been worked out by Peterson and Munson [1962] in plants having from 0 to 5 B chromosomes, finding negative results but some indication of an effect on pollen grain size variance was observed. Kato [1970] found a negative effect of B's on both pollen grain size and its variance, in plants of Nayarit 39 of the race Reventador having from 0 to 11 B chromosomes. However, he [Kato, 1970] found a significant correlation between number of B chromosomes with both days to male flowering and plant height; the correlation was positive for the former and negative for the latter. Darlington and Upcott [1941] consider that in maize populations B chromosomes are in a state of equilibrium due to a selective force favoring the maintenance of them and compensating the loss due to irregularities at mitosis and to non-pairing at meiosis.

The inheritance of B chromosomes in maize became clarified by the works of Roman [1947a,b, 1948, 1949] who, by using different A-B translocations and genetic markers on the A chromosomes involved in the translocations, has demonstrated that B chromosomes undergo non-disjunction during the second mitosis of the microspore producing individual pollen grains with two dissimilar gametes. It has been shown that the B^A chromosome carrying the B centromere is the one that undergoes non-disjunction while the A^B chromosome disjoins normally. However, the B^A chromosomes undergo non-disjunction only in the presence of A^B [in which the B segment comprises most of the distal heterochromatic region] chromosome, indicating that the distal heterochromatin of B chromosomes contains the factor[s] responsible for the non-disjunction of the proximal segment

[Roman, 1949]. Also, Roman [1948], by using the TB-4a translocation, has shown that the gamete carrying the hyperploid condition [$4^B B^4 B^4$] preferentially fertilizes the egg and the hypoploid gamete [4^B] the polar nuclei. Subsequent studies by several investigators have confirmed Roman's results [Roman and Ullstrup, 1951; Blackwood, 1956; Catcheside, 1956; Longley, 1956; Carlson, 1969, 1970, 1973; Ward, 1972, 1973a,b; Ghidoni, 1973].

Ward [1973a], by using the TB-8a translocation in which the breakage of the B chromosome occurred at the distal junction of the bulky heterochromatic segment and the small "relatively euchromatic" portion, has shown that this distal "relatively euchromatic" portion is the control site of the non-disjunction of B chromosomes, confirming the finding of Roman [1949].

By incorporating two A-B translocations, TB-4a and TB-9b, into the same plant, and by following genetically the segregation of the two B^A chromosomes at second mitosis of the microspore, evidence was obtained favoring the hypothesis that B chromosomes migrate at random to the poles, and therefore B chromosomes confer the ability for the gamete carrying them to preferentially fertilize the egg. In the same set of experiments, it was also shown that, in the presence of several B's in the male parent, the ability to perform preferential fertilization disappeared, suggesting this as a probable mechanism for controlling the excessive accumulation of B's in the population [Carlson, 1969a]. The finding of a line in which no preferential fertilization occurs when pollinated by an A-B translocation carrier indicates that the process of preferential fertilization is genetically controlled [Carlson, 1968, 1969a]. In reciprocal crosses between plants with one B chromosome and plants without B chromosomes, Kato

[1969] has preliminary data suggesting a control of the fertilization process by the female genotype.

Another interesting and unusual phenomenon found while using the A-B translocations of Roman is that observed by Bianchi, et al. [1961] who studied the stability of B chromosomes in the endosperm and the sporophyte development. They found that large sectors showed the loss of the B^A chromosomes, although in rather low frequencies. They attributed the loss to non-disjunction in somatic mitosis. Later investigations have confirmed and further substantiated the above finding. Carlson [1970, 1973a] also observed the large sectors showing the loss of B^A chromosomes on both endosperm and sporophyte, but cytological examinations have disclosed that B^A isochromosome formation was the cause of the losses. He suggested that "both non-disjunction and isochromosome formation are alternate products of the same event", that is, the "stickiness" of the centromere region. Another derivative of B^A chromosome, the unstable ring chromosome, was found by Carlson [1973a] and Ghidoni [1973]. This unstable ring chromosome behave in a similar way as the breakage-fusion-bridge cycle of McClintock [1941, 1948, 1950] producing mosaic patterns in the endosperm and the plant.

It has also been found that B chromosomes affects A chromosomes by increasing the recombination rate of the latter [Hanson, 1961, 1962, 1969; Rhoades, 1968; Nel, 1969, 1973; Chang and Kikudome, 1971a,b, 1974; Ward, 1973b]. However, Bianchi, et al. [1962] studied chromosome 9 heterozygous for the markers vg2, sh, and wx in plants with and without B chromosomes, finding no effect on recombination frequencies in the tested regions.

This enhancement of recombination in A chromosomes by the presence of B chromosomes has been found to be additive with the increase in number of B chromosomes [Rhoades, 1968; Hanson, 1969; Nel, 1969, 1973]. However, Chang and Kikudome [1971a, 1974], working with the vg2-sh-bz-wx region of chromosome 9, found that odd and even numbers of B chromosomes induce different recombination frequencies and that this effect depends on the knob constitution of the A chromosomes. In the megasporocytes of the homozygotes for the small knob, an even number of B's maintained the same recombination rate as that of no B's, but the odd numbers reduced the frequency of recombination in the distal region. In the proximal region, an even number maintained the same recombination frequency as that of no B's, and the odd numbers increased the rate of recombination. On the other hand, the odd-even effect in the heterozygotes for the large-small knobs was the opposite as that given above for the homozygous small knobs. Furthermore, the odd-even effect was more pronounced in megasporocytes. On the contrary, Nel [1969, 1973] has shown for the a2-bt-pr region of chromosome 5 that the effect of B chromosomes on recombination not only is additive, but the increase is greater in microsporocytes.

Another still controversial aspect is that Hanson [1969] for chromosomes 3 and 9, Rhoades [1968] for the Tp9 chromosome, and Chang and Kikudome [1971a,b, 1974] for the short arm of chromosome 9, found that the presence of B chromosomes cause a shift in the recombination rate from distal to proximal regions. However, Nel [1973] obtained data for chromosomes 5 and 9 showing that the proximal region is responsive to the presence of B chromosomes increasing recombination, but the distal regions are insensitive and no change in recombination frequencies occurred.

Since Chang and Kikudome [1971b] have presented evidences that there is qualitative differences regarding preferential segregation and recombination enhancement abilities among knobs, it seems probable that the differences in recombination frequencies found by Hanson [1969], Rhoades, [1968], Chang and Kikudome [1971a,b, 1973] and Nel [1973] were due to differences in the knob constitutions of the materials used by them.

The next problem regarding the recombination enhancement by B chromosomes is where the factor[s] responsible for the increase are localized in a given segment of the B chromosomes. This has been clarified by Ward [1973b] who by making use of stocks having the homomorphic transposed chromosome 9 [Tp9] but heterozygous for the c-wx genes, and three A-B translocations [Tb-4a, TB-6a and TB-8a] having the breakpoint at different positions on the B chromosome, was able to show that, with the exception of the most distal "relatively euchromatic" segment, the whole B chromosome is active in the enhancement of recombination rate.

Another unusual effect of B chromosomes is that found when a plant homozygous for endosperm recessive markers of chromosome 3 [a, sh2] without B's was pollinated by another plant homozygous for the dominant alleles and having B chromosomes; among the kernels obtained, some appeared with the recessive phenotype and further tests have shown that there was no correspondence between endosperm and embryo genotypes. Meiotic analysis of the plants grown from these unusual kernels disclosed the fact that the chromosome 3 was trisomic for its long arm [Rhoades, Dempsey and Ghidoni, 1967]. Further genetic tests with markers involving the whole long arm of chromosome 3 [gl6, lg2, a] have shown that genes distal to the knob always were missing in the endosperm of unusual kernels, but the proximal genes may or may not be present. They also found that with one B in the male parent, the loss frequency was very low, and with two B's there was a significant increase in loss, but with more than two B's, no further increase in the rate of loss occurred. Rhoades, Dempsey and Ghidoni [1967] postulated the hypothesis that when chromosome 3 is knobbed, in the present of two or more B chromosomes it is subjected to breakage with the loss of a variable segment during the second microspore mitosis. Also the knob size has an important role in determining the loss frequency, and therefore the knobless chromosomes should undergo almost no loss. Furthermore they suggested that the late replication of the knobs at the second microspore mitosis leads to the formation of a dicentric bridge, the rupture of which produces the hypo and hyperploid condition in the resulting two gametes. This mechanism explains the behavior of genes proximal and distal to the knob and the non-correspondence of the genotypes of the endosperm and embryo. In a series of experiments carried on later, Rhoades and Dempsey [1972, 1973] have substantiated the earlier results by obtaining further data with other chromosomes and given much evidence supporting the validity of the hypothesis.

Rhoades and Dempsey [1972] have shown that B chromosomes and knobs interact in producing a loss of chromosome segments only when they are together with a favorable background of genetic modifiers. As they correctly indicated, most probably there is no kind of correlation between knobs and B chromosome frequencies as shown earlier by Longley and Kato [1965]. Since the interaction knob-B chromosome is genetically modified, there is the possibility of selecting maize populations with different combinations of knobs and B chromosomes constitutions. Further support of this possibility can be found in Longley and Kato [1965] but especially in the fact that a maize variety, Nayarit 39, of the race Reventador exists possessing medium and large knobs as well as B chromosomes in very high frequencies, with an average of about 12 knobs [range 8 to 15] and 6 B's [range 0 to 13] per plant [Kato, 1964, 1965, 1970]. Moreover, this possibility could be extended to the B chromosome effect on recombination rate, since Chang and Kikudome [1971a,b, 1974] have shown the existence of knob-B chromosome interaction affecting recombination frequency. In this regard, Bianchi, Ghatnekar and Ghidoni [1963, 1964] found a negative correlation between B chromosomes and knob numbers in Italian maize, but as they indicated, because of the inadequacy of the samples with B chromosomes, the above conclusion is tentative.

Chromosome Knobs

General nature. Since their earliest studies the knobs were found to be located at fixed positions on the chromosomes, so that, although their nature was unknown, they have been used as cytological markers in many investigations.

By use of a large knob terminating the short arm of chromosome 9, McClintock [1930] was able to show that a translocation involved the chromosomes 8 and 9. This study was the basis that led to the classical investigation of Creighton and McClintock [1931] in which they demonstrated in maize that genetical crossing-over is the result of a physical exchange of chromosomal segments. Again a knob was a critical cytological marker.

Subsequent studies by McClintock [1932] showed the usefulness of the knobs as markers for identifying and interpreting the mitotic and meiotic behavior of whole chromosomes and chromosomal segments.

In his cytological observations in hybrids between maize and Florida teosinte, Beadle [1932] has reported the presence of 11 terminal knobs on the chromosomes. His mitotic karyotype of Florida teosinte showed some differences with that of McClintock [1929] for maize, but as Beadle [1932] stated, the stages studied were not adequate for making this type of comparisons because the lack of knowledge on homology between teosinte and maize chromosomes.

The first complete idiogram of the pachytene chromosomes of maize has been published by McClintock [1933] in which there are 11 knobs placed in various chromosomes. Also she established that the stickiness shown by the centromeres and the knobs of non-homologous chromosomes is different in nature from the synaptic association of homologous and non-homologous chromosomes.

Further investigations of McClintock [1938a,b, 1939, 1941, 1951] with ring chromosomes and modified chromosome 9 which carry on the phenomenon of the breakage-fusion-bridge cycle, have shown that chromosomal segments can be deleted or duplicated. When the duplicated segment carries a knob, this knob appears duplicated but unchanged. Also when a breakage occurs in the knob, the two parts are transmitted unchanged according to the size after the breakage. These results clearly indicate that knobs, when present, are structural components of the chromosome organization and that they are inherited precisely in the same way as the genes [Rhoades and McClintock, 1935; Rhoades, 1955].

With the basic information on the recognizability of the pachytene chromosomes of maize as given by McClintock [1930, 1933], more extensive studies on the chromosomes of maize and teosinte can be made. Longley [1937] carried on this task with studies of different varieties of teosintes. He found that Guatemalan teosintes have only terminal knobs, both in most of their long and short arms. In contrast to this, he found the Mexican teosintes have mostly internal knobs, although some terminal knobs were found in the short arms of several chromosomes. He also found that Florida teosinte had a similar knob composition as that of Southern Guatemala teosintes, confirming the origin of the former teosinte from the latter one. It was reported by Longley [1937] as 18 terminal knob positions for the Guatemalan teosintes and 21 for the Mexican teosintes.

Some interesting suggestions were proposed by Longley [1937]. First, that knobs are simply large chromomeres, although he did not mention any possible mechanism for enlarging chromomeres into knobs. Secondly, that the chromosomes become longer in the presence of knobs, and this suggestion was based on his observations that when a bivalent is heterozygous for an internal knob, the region of the knob position tends "to bend sharply or to leave an open loop or to push the knob to one side". In this regard, and referring to the short arm of chromosome 9, McClintock [1939] has stated that "the knob substance lengthens the chromosome at its end but does not add necessary genic material". Contrary to this idea, Maguire [1962], comparing chromosome arms with and without knobs, concluded that "the knobs did not detectably influence the variability in length of the chromosome arms on which they occurred and generally did not contribute measurably to length". However, she also realized that there is no way to know whether this similarity is due "to integrating control mechanisms in the corn nucleus or to sampling error or inadequate sensitivity of statistical tests". Thirdly, Longley [1937] suggested that knob material is genetically inert, which in essence agree with McClintock's statement given above. This suggestion was based mainly on an observational similarity between knob stickiness and B chromosome non-specific pairing, and the fact that apparently B chromosomes do not affect the maize plant phenotype. However, as already shown above, this presumed inertness of knobs and B chromosomes is no longer believed to be the case.

Frequently it is found that knobs on different chromosomes associate in forming a mass of heterochromatic material during pachytene, but it is a temporary phenomenon since the knobs tend to separate beginning in diplotene. Similar stickiness is shown by the centromeres [McClintock, 1933; Rhoades, 1955]. Also the knob and centromere associations are not the causative factors for the clumping of pachytene chromosomes, since the former can be observed equally well in clumped and in well spread pachytene material [Wellwood and Randolph, 1957].

It has been established that the position and size of knobs are constant features for a particular plant, but variable from plant to plant and from variety to variety [Kato, 1961, 1964; Kato and Blumenschein, 1967; Longley, 1937, 1938, 1939; Longley and Kato, 1965; McClintock, 1933, 1959, 1960; Rhoades and McClintock, 1935; Ting, 1958a, 1964; and others].

The Feulgen technique is specific for staining DNA. By using this technique, Morgan [1943] found a correlation between number of chromosome knobs and B chromosomes, as determined at the pachytene stage, and the number of chromocenters in interphasic nuclei of the same plant, demonstrating for the first time that those chromosome structures that were formerly referred to as deeply stained or pycnotic bodies actually have a high concentration of DNA and therefore are of heterochromatic nature.

Based on measurements of pachytene chromosomes from 14 different maize varieties from several United States Indian and Mexican localities, Longley [1939] concluded that the distribution of knobs along the length of the chromosomes is not at random, but they are located at points of maximum capacity of the knob-forming power, which depends on the distance from the centromere. He interpreted this change in the knob-forming ability in the sense that each chromosome arm has a gradient. However, this idea is invalidated by the fact that there is no experimental evidence supporting it. When knobs are changed in position within a chromosome, or from one chromosome to another non-homologous one by inversions or translocations, they maintain their size. Similarly, when a knob is broken into two different portions, each maintains the original size after breakage when transposed to different positions [McClintock, 1932, 1938a, 1939; Rhoades and McClintock, 1935; Rhoades, 1955].

Lima de. Faria and Sarvella [1962] think that the chromosome phenotype is the product of the interaction of the genetic endowment of the chromosomes with the cellular microenvironment, and that the result of these interactions is the presence of a chromosome gradient on both sides of the centromere which has specific relations to other parts of the chromosome arms. Also they assumed that any chromosome aberration, such as a translocation or an inversion, should change these gradients so that the chromosome phenotype is changed and can be subjected to differential selection. However, the credibility of this hypothesis, as with Longley's gradient hypothesis of knob formation, is shaken by the fact that the knobs, even the small knobs or the large chromomeres, maintain their original identity when changed in position within the same chromosome arm or between different arms or even between non-homologous chromosomes.

Origin of knobs in Zea. The first theory about the origin of cultivated maize that considered the knobs as an important component was the so-called "Tripartite Theory" advanced by Mangelsdorf and Reeves [1939] and further discussed by Mangelsdorf and Cameron [1942], and Reeves and Mangelsdorf [1959a]. They postulated that the original wild maize was knobless and that it was domesticated in South America. This knobless maize was spread by man to Central American regions where it met with Tripsacum having many terminal knobs. Through hybridization of Zea and Tripsacum, and backcrossing of the hybrids to Zea, the new genus, Euchlaena, originated and also new knobbed maize varieties were formed. Therefore, the knobs found in the modern races of maize and of teosinte, being of Tripsacum origin, could be used as a measure of the degree of introgression of Tripsacum genes into Zea. This would be so, if a further assumption is made, that the knobs were not introgressed alone, but the knobs carried with them some adjacent chromatin segments.

There is one major difficulty in accepting the above ideas. That is, the fact that in maize and in the Mexican teosintes most of the knobs are intercalary while Tripsacum has all its knobs terminally located in the chromosomes. According to Cooper and Brink [1937] and Rhoades and Dempsey [1953], there is no evidence that a significant amount of structural changes exists in the chromosomes of maize which could explain the shift of knobs from terminal to intercalary positions after their introgression.

Reeves [1944] determined the numbers of knobs of different maize races representing regions of North, Central and South America in an effort to find relationships between number of knobs and proximity to Central America and the Andean region of South America. He found a significant negative correlation with the first location, but the second failed to show any correlation and he concluded that the correlation found further supports the "Tripartite Theory". In this regard, the findings of Brown [1949] seem to be in contradiction of the "Tripartite Theory" because the Northern Flints of the United States that are claimed to show a high Tripsacum influence actually have few knobs. He concluded that more data must be obtained before the knobs can safely be considered as a "reliable indicator" of the degree of Tripsacum introgression into Zea. Randolph [1955], based on the fact that Tripsacum australe from South America is completely knobless according to Graner and Adison [1944], has stated "that the absence of knobs among Andean varieties of corn cannot be interpreted as evidence that admixture with Tripsacum has not occurred", suggesting that the knobs are not necessarily good indicators of Tripsacum germplasm in maize. More recently, several investigators have expressed their disagreement with the theory of Mangelsdorf and Reeves [1939], that knobs in maize and teosinte are of Tripsacum origin. It is interesting to note that Ting [1960] observed a Tripsacum australe from Colombia having few knobs and furthermore he reported some internal knobs in both T. australe and T. laxum.

Because T. dactyloides was crossable with maize and the number and position of the teosinte knobs are intermediate between maize and Tripsacum, Reeves and Mangelsdorf [1959a] concluded that the knob data "is one of the several characters which may be explained by the view that teosinte is a hybrid combination of knobless, pure corn and a form of

Tripsacum similar to T. dactyloides with many knobs". Galinat [1971] has expressed scepticism "because this interpretation is based on a broad consideration of the genus Zea, including maize from outside the distribution range of teosinte, and a narrow consideration of the genus Tripsacum in the form of a single species, their conclusion is open to serious question". Also deWet, et al. [1972] point out that the possibility for maize knobs to be of Tripsacum origin is very low because even though the Tripsacum genes can be transferred to maize, the experimental observation is that during repeated backcrossing of the Zea x Tripsacum hybrid to Zea, the Tripsacum chromosomes are rapidly eliminated, and furthermore there is selection against introgression in the gametophytic and sporophytic phases.

It seems, therefore, that most of the evidence available at present tends to support the idea that the knobs in modern maize are not of Tripsacum origin, but they are present in maize because they stem from the teosinte or teosinte-like maize ancestor.

Knobs and the origin of races of Zea. The knob number has been determined in the studies of many students of maize and teosinte. In most of the cases, it has been considered as just another characteristic and used along with the usual morphological or physiological traits in the characterization of races. However, as mentioned above, the position, size and homozygosity-heterozygosity of the knobs present in different populations is variable and, consequently, similar knob numbers might be composed of completely different knob types and, therefore, they are not comparable. Nevertheless, in spite of this limitation, the use of this characteristic has given, in several cases, important information regarding relationships between races of different geographical origin.

The study of Longley [1938] with the North American Indian maize varieties opened the way, for the first time, the use of knobs as characteristics to indicate the geographical origin of a given variety and, consequently, of its relationships to other varieties. He found that the maize populations from the southwestern United States had the highest knob endowment, and those from the northern and northeastern had almost knobless chromosomes; the maize races from the southeastern regions were found as intermediates. Similar studies of Brown and Anderson [1947, 1948] and Brown [1949] have shown that the maize varieties of the Corn Belt with 1 to 8 knobs were derived through the hybridization between the Southern Dent varieties having from 4 to 12 knobs and the Northern Flint varieties with number of knobs ranging from 0 to 5.

In the description and classification of the races of maize in Mexico by Wellhausen, *et al.* [1951, 1952], besides using 44 morphological and physiological characters of the plants, tassels and ears, made use of the knob numbers. In regard to the knobs they found that all Ancient Indigenous and Pre-Columbian Exotic races studied have a relatively low number of chromosome knobs, usually six or less; all Prehistoric Mestizos and Modern Incipient races, with the exception of Conico, have a relatively high number of knobs, usually more than six. They also stated that an increase in the knob seemed to have been favored by natural selection in the development of the Mexican races of maize, and that there is some indication that when two races cross, there is a tendency for knobs of both parental races to accumulate in the progeny of the hybrid.

Following the work of Wellhausen, *et al.* [1951, 1952], a series of studies giving the knob numbers of different races of maize in the world appeared; Roberts, et al. [1957] for races in Colombia; by Wellhausen, et al. [1957, 1958] for races in Central America; by Suto, et al. [1956] and Suto (1957, 1958, 1959, 1960] for races in Asia; by Moreno and Grobman [1958, 1960] and Grobman, et al. [1961] for races in Peru; by Brown [1960] for races in the West Indies; by Ramírez, et al. [1960] for races in Bolivia; by Timothy, et al. [1961] for races in Chile; by Tavcar [1961] for races in Yugoslavia; by Bianchi, et al. [1963] and Ghatnekar [1965] for races in Italy; and by Timothy, et al. [1963] for races in Ecuador.

Kato [1961] studied a number of presumed primitive races of maize from Mexico, Central America and South America, finding that these races can be divided into to main groups: the first includes races such as Nal-Tel, Chapalote, Pollo, and Pira consisting of plants with large knobs in high numbers, and a second group of races like Palomero Toluqueño, Confite Puntiagudo, Pisinkalla, Pororo, Canguil, and Enano comprised of plants carrying low numbers of small knobs. No details on the homozygosity or heterozygosity of the knobs were determined.

The complete utilization of all the information that knobs can offer, that is, the knob position, the knob size, the relative frequencies of different knob types, along with the geographical and racial distribution of these knobs, have been done for the first time by McClintock [1959, 1960] whose data for races of Bolivia, Chile, and Ecuador were published in Ramírez, et al. [1960], and Timothy, et al. [1961, 1963] respectively.

In the preliminary studies on the chromosome morphology of different races of maize in Latin America, McClintock [1959, 1960] concluded that there is a possibility that many of the present races of maize have had an independent origin from different centers. After the spread by migration and introduction into new regions, probably in different times, the independently formed races could have hybridized with races originating in other centers, giving rise to new racial types. Once the basic knob constitutions of the different original germplasm of the centers are known, it would be possible to determine the migration paths followed by each of them. Furthermore, based on chromosome morphology, it would be possible to learn the degree of relationship existing among the races within and between different geographical regions.

Further extensive research on chromosome knobs in Latin American races of maize was carried on by Kato [1961, 1964, 1965], and Longley and Kato [1965], but unfortunately these data were analyzed and published mostly in terms of knob numbers alone, rather than knob position, and so the results are of limited value.

Later on still more extensive knob determinations of races of maize from all the American countries were undertaken and analyzed, including all the previous available data by McClintock, Blumenschein and Kato [unpublished] and only the general preliminary results and conclusions were given by Kato and Blumenschein [1967]. The main objectives of this study were to determine the different distinct knob complexes, their centers of origin, and the major migration paths followed by these knob complexes, based on the proposal of McClintock [1959, 1960]. In total, nine knob complexes were determined. Two of them were localized in the highlands of the Central Mesa of Mexico, one completely knobless [Knobless complex] and the other having a predominance of large knobs [Palomero Toluqueño complex]; one complex [Tuxpeño complex] with a predominance of medium size knobs in all the chromosomes was centered in central eastern coast of Mexico; a third one [Zapalote Chico complex] was localized in southern Mexico with predominance of many large knobs; another complex having large knobs [Pepitilla complex] was found in the Balsas Basin in Mexico; two complexes were found in Guatemala, one in the highlands [Small Knob complex] with a predominance of small knobs, as the name indicates, and a second one in the southern lowland regions with a predominance of many large knobs; in central regions of Venezuela, a complex having many large knobs was found [Venezuelan complex]; and, finally, in the highlands of the Andes of South America, a peculiar complex [Andean complex] was determined by McClintock [1959] which has only two small knobs on the long arms of chromosomes 6 and 7. The major conclusion has been that the original populations of each of these knob complexes were the results of a polycentric domestication of a more primitive wild maize ancestor that already was differentiated into various racial types adapted to different environments. By further differentiation, migration and hybridization after domestication of the knob complexes, the modern cultivated races of maize were derived.

The concept of multiple domestication was independently arrived at by Randolph [1959] and McClintock [1959], and later supported by Mangelsdorf and Galinat [1964], Mangelsdorf and Sanoja [1965] and Mangelsdorf [1974].

The knob constitution of teosinte plants have been studied mainly by Longley [1937], Beadle [1932], Ting [1958a, 1964] and Wilkes [1967]. The information given for the different races of teosinte have been mostly descriptive and limited, but nevertheless the following knowledge has been gained from these studies: 1] Mexican teosintes have mostly intercalary knobs, although some are terminal; 2] there are Mexican teosintes, such as Nobogame, that are almost knobless, but the majority of them have a high number of knobs; 3] Guatemalan teosintes, on the contrary, have many knobs, all of them in terminal positions on both the long and short arms of the chromosomes; 4] Northern Guatemala teosintes have small knobs on the long arms of chromosomes 7, 8, 9 and 10, or are knobless, while the short arms have large knobs, except chromosome 10; Southern Guatemala teosintes, on the contrary, have large knobs on the long arms of these chromosomes and the short arms are completely knobless; 5] the perennial teosinte is practically knobless, having only large chromomeres at the ends of the chromosomes.

Although the Guatemalan teosintes are characterized by having only terminal knobs, Longley [1937] reported besides the terminal knobs, two small internal knobs, one on the short arm of chromosome 4 and the other on the long arm of chromosome 6, in teosinte plants from San Antonio Huixta. He suggested that "the teosinte of Northern Guatemala is more closely related to, or else more contaminated with, maize than is that of Southern Guatemala". Also Ting [1958a] observed six internal knobs on chromosomes 2, 3, 5, 6 and 7 and only 2 large terminal knobs on the short arms of chromosomes 4 and 9, interestingly, in teosinte plants also from San Antonio Huixta.

<u>Knobs and their correlations</u>. In an attempt to assess some kind of meaning to the knobs, many investigators have tried to correlate the presence of knobs with certain morphological or physiological characteristics of the maize plant.

The earliest attempt to make these types of correlations was by Mangelsdorf and Cameron [1942] who assumed that, since the knobs were of Tripacum origin according to the "Tripartite hypothesis" of maize origin, any morphological characteristic showing a correlation with high numbers of knobs should mean that it was also of Tripsacum origin. They studied a number of maize varieties from different regions of Guatemala and found that certain characters showed some association with high knob numbers and others with low knob numbers. For instance, varieties from the highlands of Guatemala had low knob numbers, and those from the lowlands possessed high knob numbers. Other types of characteristics such as size and shape of ear, regularity of the kernel rows, firmness of the cob, plant and endosperm color, size and shape of seeds, seminal root system, pubescence of sheaths, and smut infection were found showing some kind of association with knob number.

Cutler and Cutler [1948] indicated that for a long time the prominent rachis flaps were correlated with Tripsacum contaminated maize and with a high knob numbers, especially with the knob on the long arm of chromosome 3. However, by further studies of additional Guatemalan material, they found that this correlation was not always true.

In a survey of chromosome knobs in the maize varieties of the United States, Brown [1949] reported that high numbers of knobs showed a positive correlation with several ear and plant external characters such as high row number, denting, absence of husk blades, many seminal roots, and irregular rows of kernels. Among these correlations, two high knob number with irregular rowing and low knob number with glabrous sheaths, are in conflict with the correlations found for Guatemalan maize by Mangelsdorf and Cameron [1942]. One of the interesting observations of Brown [1949] is that among the United States maize varieties and inbreds similar correlations between knobs and morphological characteristics were apparent, and that these associations have not been broken down even after subjecting the Corn Belt maize to many years of breeding. This observation seems to indicate further that possibly the associations are very stable because the genes controlling the development of these characters are closely linked to the knobs. Such a linkage might be tightened because knobs inhibit crossing over as shown by Chang and Kikudome [1971b].

The correlation studies between 23 agronomical and mophological characters and knob numbers and 8 of these characters and six specific knobs in 20 North American inbred lines carried on by Vachhani [1950] failed to show any significant results. However, he suggested that the results should not be taken seriously because the range of the variation in number of knobs among the 20 inbred lines was low.

Wellhausen and Prywer [1954] found a relationship between knob numbers of inbred lines obtained from Mexican varieties of maize adapted to different altitudes and their combining ability as tested in topcrosses. They concluded that the data suggested that a relationship exists between knob number and factors for yield. High-knobbed inbred lines tend to perform better in crosses than the low-knobbed lines at low altitudes. On the contrary, at high altitudes the low-knobbed lines are better combiners.

Brown [1956] compared the knob numbers of 95 elite lines with those of 52 inbred lines developed without any selection. He found that the elite lines had somewhat higher average number of knobs and this difference was explained as due to the fact that, in the Corn Belt, selection against flint-like inbreds is carried on.

In Yugoslavia, Zea mays rostrata is usually grown in small fields surrounded by flint corn having a very low knob numbers. The inbred lines obtained from the rostrata variety have a high number of knobs, as reported by Tavcar [1957]. He concluded from cytogenetical studies of Zea mays rostrata and Zea mays indurata hybrids that there must exist a linkage between the rostrata type of grains and high number of knobs.

Ibrahim [1960] examined about 150 open pollinated varieties of maize from different parts of the world and found that there was a high correlation between high knob number and large kernel size, and also there was an indication that the high knob number is associated with denting and high kernel row number. However, when the Peruvian race Cuzco Gigante having huge kernels with a low knob numbers within the range of 0-3 knobs per plant [Grobman, et al., 1961] and the races Nal-Tel and Chapalote from Mexico with small kernels and high knob numbers [ranges from 8-13 and 10-14 respectively] as reported by Longley and Kato [1965] are considered, it seems that this correlation between knob number and kernel size is invalidated.

Plants of a population of the race Chapalote from Mexico were studied cytologically and morphologically by Murdy [1963] finding that there was statistically significant associations between two specific knobs and several morphological characteristics. The knob on the long arm of chromosome 4 was correlated with small stem diameter and many tillers, and the second knob on the long arm of chromosome 6 showed association with late pollen shedding, many stem internodes, and narrow leaves. The other

4 knobs [1L, 4S, 6La and 8L] which were segregating in the population did not show any association with the 21 plant characters analyzed.

Zvingilas [1963a, b] found an inverse relationship between the knob number and the number of nucleolar-like droplets in the microsporocytes at pachytene. She also found a positive correlation between knob number and multiple chromosome associations in diakineses.

A study of the possible associations between knobs and racial characteristics was undertaken by Blumenschein [1964] in a cross between two distinct maize types, a variety of Zapalote Chico from Southern Mexico and the inbred line Knobless Flint from the United States. The possible associations in the F_2 between ten knob positions and 15 morphological characteristics were statistically analyzed. He found 48 statistically significant cases of association between knobs and characters among the 150 associations studied. The interpretation given by him was that the associations found are evidence that genes controlling different morphological characters are closely linked to different knobs, and that because of this close linkage, the knobs can be selected during the formation of races in maize.

In 288 Italian open pollinated varieties, Lorenzoni [1965] found that some of the plant and ear characters showed increasing values with higher numbers of knobs. However, there were three specific knobs [1S, 3L and 4L] especially notable because when at least two of these knobs were present simultaneously the character difference was greater in relation to the knobless condition. He also explained these associations by assuming that the genetic factors responsible for the development of the characters are linked to the knobs.

More recently, Moll et al. [1972] have reported associations between greater ear and plant height with four heterozygous knobs [2L, 6L3, 8L and 9S] and greater yield of grain with three of these knobs [6L3, 8L and 9S]. They considered that these associations might be due to gene complexes linked to the knobs and that the knobs may have different adaptive values depending upon the kind of genes to which they are linked.

Inversions and Their Significance

The first reported inversion in maize was X-ray induced and described by McClintock [1931]. It was a long pericentric inversion on chromosome 2. Further, McClintock [1933, 1938a] reported two paracentric inversions, one naturally occurring on the short arm of chromosome 8 and another X-ray induced on the long arm of chromosome 4, and one small pericentric inversion on chromosome 4 found in some genetic stocks. Later on, several investigators have reported other inversions: Clark [1942] reported an induced pericentric inversion on chromosome 1; Russel and Burnham [1950] reported an induced paracentric inversion on the long arm of chromosome 2; Morgan [1950] studied cytogenetically three X-ray induced inversions, one paracentric type on the long arm of chromosome 4 previously reported by McClintock [1938a], and two pericentric inversions on chromosomes 2 and 5; Rhoades and Dempsey [1953] studied one paracentric inversion on the long arm of chromosome 3 existing in the Tu line they used; Longley [1961] has reported 60 paracentric and pericentric inversions for 9 of the 10 chromosomes isolated from maize material treated with ionizing radiation from different sources; McClintock [1959, 1960] found in one of the races of maize from Bolivia, and in four races from central highlands of Mexico, the same inversion in chromosome 8 as that previously reported by her

[McClintock, 1933]. The same inversion was found in a collection of the race Arrocillo Amarillo by Kato [1964, 1966] who also reported in the same material an additional paracentric inversion involving a small segment about the knob position on the long arm of chromosome 1.

Most of the basic cytological analyses of inversions in maize have been made by McClintock [1931, 1933, 1938a], and all investigators that have subsequently studied these chromosomal aberrations have based their findings and interpretations on McClintock's findings.

In her extensive studies on the nature of homologous and non-homologous associations of pachytene chromosomes, McClintock [1933] has concluded that the longer the inverted segment, the greater is the combined forces of homologous attraction in this region to overcome counter forces tending to prevent homologous associations; on the other hand, the shorter the inverted segment, the lower the frequency of the characteristic loop configuration.

Based on her studies on the paracentric inversion on chromosome 4, McClintock [1938a] gave the configurations observed at anaphase I and the explanation of the mechanisms by which these configurations resulted, as follows:

1. A single bridge and single fragment. This configuration results when a single crossover occurs between two paired homologous chromatids within the inverted segment. Two types of this configuration can be found: a] the fragment is free in the spindle, resulting when the single crossover occurs within the inverted segment, and b] the fragment appears to be attached to one of the arms of the normal chromatids of the bivalent, and is the result of two combined crossovers, one within the inverted

segment and the other in the distal segment.

2. A double bridge and two fragments. This configuration is the result of a 4-strand double crossover within the inverted segment. The two fragments are distributed at random to the two cells of the second meiotic division.

3. A free fragment and no bridge. It is the result of a 4-strand double crossover, one in the proximal segment and the other within the inverted segment. In anaphase II, only one of the cells shows a bridge and the fragment appears in either of the two cells.

4. Two free fragments and no bridge. This results from a 4-strand triple crossover, one in the proximal segment and two within the inverted segment. At anaphase II, both cells show a bridge and the two fragments are distributed at random to the two cells.

In the case of pericentric inversions, a crossing over within the inverted segment does not give dicentric bridges and acentric fragments at anaphase I as in the case of paracentric inversions, but it produces deficient-duplicate chromatids which in turn induce the abortion of the pollen and ovules that receive them. Consequently the detection of the pericentric inversions is only possible at the pachytene stage of meiosis [McClintock, 1931, 1933; Clark, 1942; Morgan, 1950; Rhoades, 1955].

The formation of bridges and acentric fragments in either meiotic anaphase I or II as a result of crossing over occurring in the inverted segment will produce deficiencies and duplications in the chromatids involved in the exchanges. Those spores receiving the deficient chromatids usually abort, and consequently the degree of pollen and ovule abortion should reflect the amount and the kind of crossing over that occurred within the inversion [Rhoades and Dempsey, 1953]. The degree of formation of bridges and fragments and, therefore, of pollen abortion, is very variable depending upon the size of the inverted segment, but also the same inversion usually shows a great deal of variability in this regard as a consequence of a variable degree of homologous pairing of the inverted segment and of the recombination, probably influenced by differences in genetic and environmental factors under which the inversion exists [McClintock, 1933, 1938a; Morgan, 1950; Rhoades and Dempsey, 1953; Kato, 1964, 1966].

It has also been shown that the degree of pollen and ovule abortion for the same inversion frequently is completely different, and in these cases usually the female side shows the lower abortion frequency. Morgan [1950] found that for the paracentric inversion In4a, the average pollen abortion was 28.2%, while the ovule abortion amounted to only 4%. This difference was attributed to the exclusion of single crossover chromatids from the functional megaspores and, the aborted ovules results mainly from 4-strand exchanges within the inverted segment [Morgan, 1950]. Similarly, in the pericentric inversion In5a heterozygotes, Morgan [1950] found an average of 28.3% pollen abortion but only 12.5% of ovule abortion. In this case he thought that crossing over occurs at higher frequency in microsporogenesis than in megasporogenesis. No difference was found for the case of the pericentric inversion In2a by Morgan [1950].

Kato [1964, 1966] has reported an average pollen abortion of 1.23% for the inversion on the short arm of chromosome 8 and 0.35% for the inversion on the long arm of chromosome 1, showing the small amount of crossing over occurring within the inverted segments. However, when both inversions were present in the same plant, the pollen abortion increased to 3.18%, suggesting some interchromosomal effect on crossing over.

In their studies on the paracentric inversion In3a, Rhoades and Dempsey [1953] have shown evidence that some of the deficient-duplicate chromosomes can be transmitted through the female side, but never by the pollen. These result from the breakage at proximal regions of the dicentric bridges through crossing over within the inverted segment in the heterozygous condition. They think that fertility of the megaspore is possible in this instance because the deficient segment distal to the inversion is very short.

The most interesting finding of Rhoades and Dempsey [1953] is that the recombination frequency within the inverted segment was reduced drastically but the proximal non-inverted segment showed a slight increase in the rate of crossing over, from 15.4% in homozygous normal chromosomes to 16.3% in heterozygotes for the inversion. In this regard, Bellini and Bianchi [1963], using two pericentric inversions [In 2a and In 9a], studied the interchromosomal effect of the inversions regarding crossing over rates and obtained evidence that in the presence of In2a, the distal Yg2-Sh region of chromosome 9 had an increased rate of crossing over, but the more proximal Bz-Wx region showed a decrease in crossing over; also the In9a increased the recombination rate in the distal Lg-Gl2 region of chromosome 2, while the proximal Gl2-V4 region showed very little change. These data clearly indicate that inversions have the ability not only to reduce crossing over within the inverted segment, but also to change the recombination rates in other regions of the same chromosome, or even of non-homologous chromosomes. Also, the data suggest that different chromosomal regions react differently to the same inversion. Whether the same segment reacts similarly in the presence of different inversions is a problem that needs further investigation.

Most of the inversions studied in maize have been artificially induced and are relatively long. There are several known cases of inversions that were not induced and of relatively small size, such as the paracentric inversion of the short arm of chromosome 8, the small pericentric inversion of chromosome 4, and the paracentric inversion on the long arm of chromosome 1 reported by McClintock [1933, 1959, 1960] and Kato [1964, 1966]. Rhoades and Dempsey [1953], after studying 90 Latin American races of maize, stated the possibility that small inversions might be more frequent in nature than the large ones, but the technique used to detect them probably was not adequate. This possibility is further substantiated by the findings of McClintock [1933, 1959, 1960] and Kato [1964, 1966].

More intensive studies on teosinte have revealed many non-induced and relatively small inversions. The interest in looking for inversions in teosinte began with the findings of Beadle [1932b] and Emerson and Beadle [1932] that in hybrids of maize with Durango and Florida teosintes crossing over between marker genes of chromosome 9 [yg2-c-wx] was completely or almost completely absent, while other chromosome segments showed normal recombination rates. These results indicated that possibly the reduction of crossing over was due to an inverted segment that included the marker genes of chromosome 9.

In hybrids between Durango and Florida teosintes with maize strains homozygous for known reciprocal translocations, Arnason [1936] has shown

TABLE 1. Relatively small chromosome inversions found in different maize and teosinte populations and already reported in the literature. Inversion In4 is of a pericentric type and all others are paracentric.

Species and place	I N V E R S I O N S							
	In1La	In1Lb	In3L	In4	In5L	In7L	In8S	In9S
MAIZE								
Bolivia	-	-	-	-	-	-	6	-
Mexico	4	-	-	-	-	-	4,8	-
U.S. Genetic stocks	-	-	-	5	-	-	5	-
TEOSINTE								
Nobogame	-	-	-	-	9	-	9	9
Durango	-	-	-	-	-	-	9	1,2,9
Chalco	-	-	9	-	-	-	9,11	9
Guanajuato	-	-	-	-	-	-	11	11
Guerrero	No	inversions	have	been	reported	so	far	
N. Guatemala	No	inversions	have	been	reported	so	far	
S. Guatemala	-	10	-	-	-	-	-	10
Florida	-	-	10	-	-	-	-	1,2,3 8,10
Perennial	-	-	-	-	-	-	-	9

1. Arnason [1936]
2. Beadle [1932]
3. Emerson and Beadle [1932]
4. Kato [1964, 1966]
5. McClintock [1933]
6. McClintock [1959]
7. McClintock [1960]
8. O'Mara [1942]
9. Ting [1964]
10. Ting [1965]
11. Wilkes [1967]

that T8-9a formed rings at diakinesis in a reduced frequency while translocations in other chromosomes showed similar ring frequencies when compared to corresponding stages of maize heterozygous for the same translocations. He also found an almost complete absence of crossing over between marker genes in the short arm of chromosome 9 in maize x teosinte hybrids, showing that some structural rearrangement, most probably an inversion, in the short arm of chromosome 9 was present in his Durango and Florida teosinte.

Further cytological analysis of pachytene chromosomes have demonstrated that actually a paracentric inversion on the short arm of chromosome 9 is present in Florida teosinte [O'Mara, 1942; Ting, 1965] in teosinte from Jutiapa and Lake Retana in southern Guatemala and from Xochimilco, Chalco, Durango, Nobogame, Guanajuato, and in the perennial teosinte in Mexico [Ting, 1958a, 1964, 1965; Wilkes, 1967].

Several other inversions have been found in different teosinte plants from Mexico and Guatemala with the exception of teosinte from northern Guatemala [San Antonio Huixta] and Guerrero [Chilpancingo and Arcelia] in Mexico by Ting [1958a, 1964, 1965] and Wilkes [1967]. A summary of the inversions found in teosinte and maize is given in Text Table 1.

It has been reported by Ting [1964] that in Xochimilco teosinte x Wilbur's Flint, those plants having In3, In8, and In9 together the frequency of loop configurations of In8 and In9 and the frequency of bridges with acentric fragments were higher than in plants carrying only In8 and In9. However, this interchromosomal effect did not occur between In8 and In9. He thinks that the best explanation is that the interchromosomal effect of In3 on homologous pairing and crossing over of In8 and In9 is due to a kind of "position effect".

The presence of the inversions in teosinte has been interpreted as devices which had an important evolutionary role because they reduced crossing over and therefore tend to block gene combinations which have adaptive values [Ting, 1964], or which serve as partial isolating mechanism between maize and teosinte [Wilkes, 1967]. In this regard, it is of interest to note that Ting [1965] reported that "using Florida teosinte as donor parent, it was unsuccessful to incorporate its In9 into maize through repeated backcrosses to the latter [unpublished results]".

Theories on the Origin of Maize

Several theories have been proposed as to the origin of maize. Ascherson in 1895 [Mangelsdorf and Reeves, 1939] proposed that maize was domesticated from teosinte. The idea of a common ancestry for maize, teosinte and tripsacum was advanced at the beginning of this century [Weatherwax, 1918]. The hypothesis that cultivated maize was domesticated from wild maize is part of the tripartite theory [Mangelsdorf and Reeves, 1939]. The "amphiploid" theory proposed by Anderson [1945] postulates that primitive maize originated in southeastern Asia through the hybridization and chromosome doubling of two species each with 5 pairs of chromosomes, such as in some species of Coix and Sorghum. Andres [1950], after having discovered in Argentina a weak form of pod corn called "semivestidos", suggested that this type of maize was the ancestor of modern maize. Finally Singleton [1951] suggested that the mutant called "corn grass" may reveal some of the primitive traits of the ancestral type.

Goodman [1965], after having thoroughly reviewed the current theories on the origin of maize, concluded that "until more is known about the genetic and morphological relationships between the American Maydeae, the Oriental Maydeae, and the Andropogoneae, the writing of a history of the evolution of maize and/or its relatives will continue to resemble an attempt to complete a jigsaw puzzle with three-quarters of the pieces missing". It seems that since the time when this conclusion was written, many pieces of the jigsaw puzzle have been found, although it does not mean that the final picture has been completed. However, a better view of the picture seems to appear before us now than ten years ago, which strongly suggests what kind of picture the final one will be.

At the present time most of the thinking regarding the origin of maize considers only three of the above mentioned theories [Galinat, 1971]. The oldest teosinte theory is supported by Beadle [1972], Galinat [1971, 1972, 1974a], Iltis [1972], deWet and Harlan [1972]; the tripartite theory in its modified form is maintained by Mangelsdorf [1974]; and the theory of the common ancestry has been kept alive by Weatherwax [1955] and Randolph [1952, 1955, 1959].

The tripartite theory postulates: 1] that cultivated maize was domesticated from a wild knobless pod-popcorn; 2] that the domesticated knobless maize hybridized with Tripsacum having many terminal knobs giving origin to a new plant type, teosinte; 3] that the direct hybridization of maize with Tripsacum or the introgression of Tripsacum germplasm via teosinte into maize gave rise to the majority of the modern maize types existing in America [Mangelsdorf and Reeves, 1939, 1959a,c,d; Mangelsdorf, 1947, 1958, 1961, 1974; Reeves and Mangelsdorf, 1959b].

The main evidence for considering that the ancestral corn was a pod-popcorn are that: 1] the floral bracts which cover the grains is a primitive characteristic almost universally found in wild and cultivated grasses; and 2] a weak form of the popcorn character is claimed to persist among the present races of maize considered as primitive [Mangelsdorf and Reeves, 1939a; Mangelsdorf, 1947, 1958, 1974].

That the pod corn is monstrous and sterile have been given by Weatherwax [1955] and Randolph [1955, 1959] as evidences that it could not be wild corn because a corn with these characteristics would not be able to survive in nature. This objection to the pod corn postulate has been explained by the finding that the Tu locus is complex and that there are several alleles and modifier genes which make the tunicate character less monstrous and more fertile [Manglesdorf, 1947, 1958, 1974; Mangelsdorf and Reeves, 1959a; Mangelsdorf and Galinat, 1964]. These findings demonstrate the fact that the phenotypic expression of any gene locus can be modified in a given way by assembling an appropriate genetic background. Brieger, et al. [1958] have also objected that since full tunicate is not found in special racial types but it can occur in any ordinary field corn, it seems probable that it is a recent mutation.

The major difficulty of the tripartite theory, however, seems to reside in its second postulate, that teosinte was originated from the hybridization between a knobless wild corn with Tripsacum having chromosomes with many terminal knobs, and this part has now been rejected by one of its authors [Mangelsdorf, 1974]. Some of the historical objections to this defunct postulate follow. The known maize-Tripsacum hybrids have been obtained artificially and only by the aid of special techniques which makes the natural occurrence of the hybridization improbable. The hybrids obtained are usually highly sterile. In fact, no natural maize-Tripsacum hybrid has ever been found and the artificial hybrids have not been known to produce any progeny plant types resembling teosinte [Weatherwax, 1955; Randolph, 1952, 1955, 1959; deWet, Harlan and Grant, 1971; deWet and Harlan, 1972]. Also the fruit case of teosinte is much more specialized and differs from that of Tripsacum regarding the degree of induration, the development of root and shoot pores, and in the method of rachis disarticulation, characters that have been important in the evolutionary survival of teosinte in the wild. Therefore, if teosinte is the hybrid product of maize and Tripsacum, as the tripartite theory once postulated, it is difficult to explain satisfactorily why teosinte and Tripsacum fruit cases do not show closer similarity in their morphology [Galinat, 1970, 1971].

deWet, et al. [1972] have stated that "although gene transfer from Tripsacum to maize is possible, it will be extremely difficult to accomplish in nature. Hybrid seeds have poorly developed endosperm, and the probability that they would produce viable offspring in natural competition is small indeed. Moreover, both gametophytic and sporophytic selection against introgression operates as long as any perceptible trace of Tripsacum contamination remains".

Another evidence that weakened the concept of a hybrid origin of teosinte is related to the controversial findings regarding the fossil pollen grain assignment to either maize or teosinte. Barghoorn, et al. [1954] and Irwin and Barghoorn [1965], by examining fossil pollen from deep Bellas Artes drill cores in Mexico city, have found large pollen grains which they interpreted as pollen grains of an ancient maize that was growing there long before domestication of this plant. However, there are some studies that contradict this conclusion. Kurtz, et al. [1960] found that environmental factors influence size as well as both axis length and pore diameter of the pollen grains, concluding that differentiation between pollen of maize, teosinte and Tripsacum based on these characteristics is not always reliable. Also Galinat [1973] has reported data on pollen grain size showing that teosinte pollen has a wide range in variation and that three pollen samples measured [one Mexican and two of Guatemalan teosintes] had a larger mean diameter than pollen from the lowest level of the Bat Cave. These findings clearly show that the fossil pollen of Mexico city not necessarily belongs to maize plants, but it could equally well be assigned to teosinte.

Many archaeological maize remains have been found in different places in America, and among the most numerous and thoroughly studied probably are those of Mangelsdorf and Smith [1949] and Mangelsdorf, Dick and Camara-Hernandez [1967] at Bat Cave in New Mexico; those of Mangelsdorf and Lister [1956] at Swallow and other caves in northwestern Mexico; and those of Mangelsdorf, MacNeish and Galinat [1956, 1964, 1967] at La Perra Cave in eastern Tamaulipas, and in several caves in the valley of Tehuacan in Mexico. In all these cases, it has been observed that the oldest remains at each locality invariably failed to show signs of morphological characters called "tripsacoid" in the form of indurated rachis and glumes of the cobs. This fact has been interpreted that the early domesticated maize was not contaminated with Tripsacum germplasm, and that later this introgression occurred directly from Tripsacum or indirectly by way of teosinte. The nature of the present Tripsacum species has been interpreted in two ways.

Weatherwax [1918, 1935, 1955], based on morphological grounds, has proposed that maize, teosinte, and Tripsacum were originated from some common ancestor by "ordinary divergent evolution" which produced the differences among them by "differential abortion of organs during development". This hypothesis also implicates that the present Tripsacum species are forming a polyploid series with an ancestral chromosome number of x=9 which, in turn, originated in some way from the ancestral stock of the American Maydeae having x=10. The second interpretation, more widely accepted and better supported by experimental evidence, considers that the n=18 Tripsacum species are of ancient allopolyploid origin. The first version of this hypothesis regards the parents of Tripsacum to be two species of an Andropogonaceous plant, including the genus Manisuris [Anderson, 1944b; Stebbins, 1950]. After cytogenetic comparisons of the genomes of maize and Tripsacum, Galinat et al. [1964] and again modified by Galinat [1974b], suggests that Tripsacum originated as a amphidiploid from a wider cross between a Manisuris-like species and a Zea-like species. This hypothesis is supported by studies of intergenomic mapping as follows: 1] there are several Tripsacum chromosomes that appear to be completely alien in a cross-mapping comparison to maize [or teosinte], and 2] although there is extensive repatterning between the genomes, maize and Tripsacum do share some short linkage groups in common [Galinat, 1974b]. If some species of the genus Zea is a parent of the genus Tripsacum, then obviously Zea is older than Tripsacum.

It is clear, however, that Tripsacum is also a very old genus, as further evidenced by its highly developed polyploid series with a wide geographical distribution from North America through Central America up to Brazil, Bolivia, and Paraguay in South America [Cutler and Anderson, 1941; Tantravahi, 1968; Randolph, 1970]. Consequently, the possibilities for introgression of Tripsacum germplasm into maize should have existed for long periods in the past. However, the archaeological maize remains show that the so-called "tripsacoid" characters appear much later, after the domestication of maize from its wild ancestor occurred. Therefore, it seems improbable that these characteristics of maize plants come from Tripsacum through introgressive hybridization, and therefore some other explanation should be found.

It has been contended by Mangelsdorf and Cameron [1942], Reeves and Mangelsdorf [1959a], and Mangelsdorf [1961, 1974], that Tripsacum introgression into maize has comprised not single independent genes, but chromosomal segments carrying knobs and linked gene complexes. One of the important chromosomal segments containing a genetic complex essential for the development of the fruit case of teosinte, a morphological character that not only distinguishes teosinte from maize, but also has had an important evolutionary role regarding teosinte survival in the wild, is located in chromosome 4. Galinat [1971, 1974b] has found that "cytogenetic comparisons of maize and tripsacum chromosomes were unable to reveal any single assemblage of loci in tripsacum corresponding to maize chromosome 4 that could contribute this vital introgression. The various loci of maize chromosome 4 are present in tripsacum but dispersed among several different chromosomes". This finding led him to conclude that "the fourth chromosome complex would seem to make the hypothesis that tripsacum is a parent of teosinte improbable, if not untenable".

The difficulties in shifting the terminal knobs of Tripsacum to intercalary positions as found in many teosinte and maize chromosomes were expressed by Rhoades [1955] and Randolph [1952, 1955, 1959] and reviewed above in the chapter on chromosome morphology.

Mangelsdorf [1974] has stated that "since hybridization between the two genera is at best rare, it may be a long time before a natural hybrid is found. In the meantime, the evidence for such hybridization must continue to remain circumstantial". Furthermore, Mangelsdorf [1974] has abandoned the part of the tripartite theory proposing a hybrid origin of teosinte. Mangelsdorf [1974] says that the main basis for his change in opinion has come from the results of electron microscope studies of pollen grains by Banerjee and Barghoorn. These studies revealed that the "spinules" are uniformly distributed on the surface of the pollen exine in the races of maize and teosinte studied, while in pollen of Tripsacum and of experimental derivatives of corn-Tripsacum hybrids, these "spinules" tend to appear in clusters, showing that neither teosinte nor Tripsacum derivatives of corn have an intermediate condition as would be expected if teosinte is a hybrid of maize and Tripsacum. Mangelsdorf [1974, p. 49] concluded that "the studies of Barghoorn and Banerjee, working with Galinat, have demonstrated beyond a reasonable doubt that teosinte is not a hybrid of maize and Tripsacum". As a substitute, Mangelsdorf [1974, p. 52] now suggests that "teosinte is essentially a mutant form of maize". As supporting evidence for this new hypothesis, Mangelsdorf [1974] says that "in a number of morphological characteristics maize is more primitive and teosinte the more highly evolved of the two". This hypothesis implies that up to the time of domestication of maize both the wild maize and its presumed derivative species, teosinte, were existing, but later the wild maize, which assumedly was widely distributed, became extinct because it was swamped out by cultivated maize. It seems that this extinction of wild maize is contradictory with the earlier statement of Reeves and Mangelsdorf [1959b] that "the tripartite theory ...... requires no ancestral types other than forms still in existence". That is, it cannot be extinct, but still in existence.

As Galinat [1971, 1972, 1974a] has clearly pointed out, teosinte and maize have specializations of their own which are well suited for adapting and surviving to different kinds of selection pressures, one imposed by natural selection in the wild, and the other effected through artificial selection. On this basis, it seems that comparisons between the specializations of these two plant species are not always valid.

Also, Galinat [1971] has shown that "with higher levels of natural heterozygosity, there is no need to assume that introgressions by wild relatives could be the only adequate source of variation to account for the adaptive responses of the original Zea population to both domestication and continued survival in the wild. Thus, there is no necessity on genetic grounds for assuming an extinction of the wild progenitor of cultivated maize". This conclusion is further supported and substantiated by the fact that teosinte shows a wider range in knob variability than maize [Longley, 1937, 1938, 1939, 1941; Rhoades, 1955; Ting, 1958a, 1964, 1965; McClintock, 1959, 1960; Ramirez, et al., 1960; Timothy, et al., 1961, 1963; Kato, 1961, 1964, 1965; Bianchi, Ghatnekar and Ghidoni, 1963; Ghatnekar, 1965; Longley and Kato, 1965; Kato and Blumenschein, 1967; McClintock, Blumenschein and Kato, unpublished].

All authorities now agree that the accumulating evidences make the hybrid origin of teosinte not only very improbable, but almost impossible. Therefore, consideration of teosinte or a teosinte-like plant as the ancestor of maize is an active area of research. This point of view is logical because teosinte is a successful existing wild plant and especially due to the undeniable and widely accepted fact that teosinte is the closest relative of maize from the taxonomic, morphologic, cytologic, and genetic point of view [Beadle, 1932a,b, 1939, 1972; Emerson and Beadle, 1932; Reeves and Mangelsdorf, 1942, 1959a; Mangelsdorf, 1961, 1974; Galinat, 1956, 1970, 1971, 1972, 1974a; Darlington, 1963; Wilkes, 1967, 1972; Iltis, 1969, 1972; deWet, et al., 1971, 1972; deWet and Harlan, 1972].

It has been shown by Bonnett [1948, 1953, 1954] and Galinat [1956, 1959, 1970] that distinct morphological organs and parts of them can differentiate from similar primordia depending upon the kind of the controlling genetic complex that becomes activated during the different parts of the phytomer and developmental stages of the individual. Obviously these controlling systems are the result of natural and artificial selection that have operated on maize populations for long periods of time. The necessary variability for selection to be effective should result basically through mutation and recombination. Therefore, similar kinds of controlling gene complexes should be able to be assembled by appropriate selection acting at the population level in time and space for differentiating two distinct species from an ancestral one. The general mechanisms for assembling these controlling systems are known [Dobzhansky, 1970; Ford, 1971; Grant, 1971]. For the specific case of teosinte and maize, Galinat [1972, 1974a] has proposed one plausible mechanism through unconscious selection during the practice of harvesting by primitive man. The harvesting process would automatically favor teosinte plants having features involving easier harvesting derived from more condensed spikes with less shattering fruit cases. This kind of disruptive selection between man and nature would canalize the potential genetic variability already present in wild ancestral populations towards is separation into two different plant types, one more useful to the needs of man and the other remaining well adapted for survival in the wild.

This artificial speciation mechanism [domestication] also makes more understandable how similar plant types can be developed by different people, in different regions, and at different times from an ancestral wild plant species probably already well differentiated into several racial types and with a wide geographical distribution. In fact, the idea of a polycentric domestication of maize is becoming more prevalent at the present time [Mangelsdorf and Reeves, 1959c; McClintock, 1959, 1960; Randolph, 1959; Grobman, _et al_., 1961; Mangelsdorf and Galinat, 1964; Kato and Blumenschein, 1967; Brandolini, 1970; Mangelsdorf, 1974].

CHAPTER III

MATERIALS AND METHODS

Teosinte and Maize Collections

In a total of 54 collections, 310 plants of Mexican teosinte from different regions were examined. Similarly, 7 collections represented by 47 plants of Guatemalan teosinte were studied. In the case of maize, 138 collections from regions of central Mexico with a total of 782 plants were analyzed. The general information about each of these teosinte and maize collections are given in Appendix Tables 1 and 2. The regions concerned here are shown in the Text Figure 1. The geographical distributions of the collections according to their original collection places are presented in Text Figures 2, 3, and 4.

Most of the teosinte seed used in the present studies were from original collections made by the author during the years 1966 through 1970 and deposited in the C.I.M.M.Y.T. [Centro Internacional de Majoramiento de Maíz y Trigo or International Maize and Wheat Improvement Center] germplasm bank. The 2 collections from Nobogame, Chihuahua, 2 from northern Michoacán, 2 from Huetamo in Michoacán, 3 from Guerrero and those of Guatemala, with the exception of one collection of the latter which was made by Dr. H. Cutler in 1940, were from sample seeds of some of the collections made by Dr. H. Garrison Wilkes of the University of Massachusetts at Boston in 1963-64 and maintained under cold storage by Dr. Walton C. Galinat at the Suburban Experiment Station in Waltham. Seed samples of 3 teosinte and 4 maize collections from El Salado in the Mazatlán area in central state of Guerrero were kindly supplied to the author by Dr. George W. Beadle of the University of Chicago who collected them in 1972.

The maize seed samples used were from collections maintained at the I.N.I.A. [Instituto Nacional de Investigaciones Agrícolas of Mexico] and C.I.M.M.Y.T. germplasm banks.

The sample seed of teosinte collections of Dr. Wilkes and of Dr. Beadle were grown at the Suburban Experiment Station during the summer of 1973. Most of the other teosinte collections were grown during the winter of 1970-71 at the experiment station that C.I.M.M.Y.T. has in Tlaltizapán in the state of Morelos. Teosinte is a short day plant so that under the summer conditions of Waltham they needed an artificial shortening of the day length in order to flower. Therefore, plants grown in Waltham were given a short day treatment by covering the plants with trash cans from 5 P.M. to 9 A.M. This treatment was started when the seedlings had about 6-7 leaves and continued for about 4-6 weeks until the tassels were differentiated.

The maize collections were grown in Mexico in different years and at several locations. However, the 4 collections obtained from Dr. Beadle were grown in Waltham along with the teosinte collections in 1973.

There are 4 teosinte and 3 maize collections given in entries 28 to 31 and 89 to 91 of Appendix Tables 1 and 2 respectively that actually are a different type of collections with respect to the others. In these cases, cytological material instead of kernels were collected directly from the maize fields in the Chalco region during the summer of 1970.

Cytological Techniques

All the cytological material consisted of young tassels taken from the plants before they emerged out from the upper leaves of the main stalks or the tillers. In the case of teosinte, in some instances the young tassels of side branches were used. Usually the tassels at this stage of development will take about 4-6 days to complete emergence from the leaves.

The tassels were killed in a mixture of 3 parts of 95% ethyl alcohol and 1 part of glacial acetic acid. They were kept in the fixative for 2 days at room temperature and then replaced once with 70% ethyl alcohol and stored in a deep freezer. However, all the cytological material collected in Mexico was kept without any refrigeration for about a week during its transportation to Massachusetts and no harmful effect was found.

The cytological observations were made in cells stained with propiono-carmine following the usual squashing technique. The knob constitution was usually determined at the mid-pachytene stage but in most of the cases, a late pachytene or even the early diplotene stages were used in order to determine the homozygosity-heterozygosity condition of the knobs.

The length measurements of the pachytene chromosomes were made by the following technique. Ten cells in each plant at mid-pachytene in which all the 10 chromosomes could be clearly followed and with their centromeres apparent were selected. A drawing of the chromosomes as observed in the cell was made by using a Zeiss type camera lucida which enables one to draw directly on the table where the microscope is located. At the same time the lines 10 u apart of a stage micrometer were drawn. These chromosome drawings and the lines of the micrometer were further amplified by projecting the drawings against a wall with an overhead type projector. Care was taken to make the projection perpendicular to the wall plane. For this purpose, several lines of known length were traced perpendicularly near the edges of the paper containing the chromosome drawings and their lengths were checked on the projected image every time a new drawing was made. Also, by maintaining the projector at the same distance from the wall, drawings with the same final magnification were obtained. The measurements on these amplified drawings were made using a map rule having a scale that gave direct readings in centimeters and millimeters with an approximation of about ± 1 millimeter. The drawings of the micrometer scale were used to make the conversions to microns.

The pollen grain counts were made by sampling many places of each slide containing pollen stained with the propiono-carmine solution. The cytoplasm and the starch grains stain dark with this solution so that it was possible to distinguish easily the normal grains from the cytoplasm and starch deficient and empty grains.

Analysis of the Knob Data

The detailed data of knob constitutions of each teosinte and maize collection are given in Appendix Tables 3, 4, 5, 6, 7, 8, 9, 10, and 11.

From previous experience with extensive maize knob data, it was known that the graphic representation of the relative frequencies of knobs on maps was an effective method for analyzing this type of data. Therefore, a similar method was followed in the present studies.

In the first place, the relative frequencies of the various knob conditions at each position for every collection was determined. Since the knob homozygosity-heterozygosity condition of each position was determined, actually the knob frequencies could be given in terms of chromosome numbers instead of plant numbers. If, for example, 12 plants were analyzed in a collection, actually the knob condition for a given position in 24 chromosomes was obtained. When less than 1/3 of the chromosomes analyzed had a given knob condition, it was considered as low in frequency for that knob condition, if between 1/3 and 2/3 as intermediate in frequency and when more than 2/3 as high in frequency. These relative frequencies were designated by conventional graphical signs and plotted on maps according to the geographical origin of the collection. Separate maps were made for every knob condition at each position.

The determination of distribution patterns was made by repeatedly comparing these maps. The pattern found for each knob condition of a given position was then compared to the patterns found for other knob conditions at other positions by following the same method. The same method was used for comparing distribution patterns between teosinte and maize.

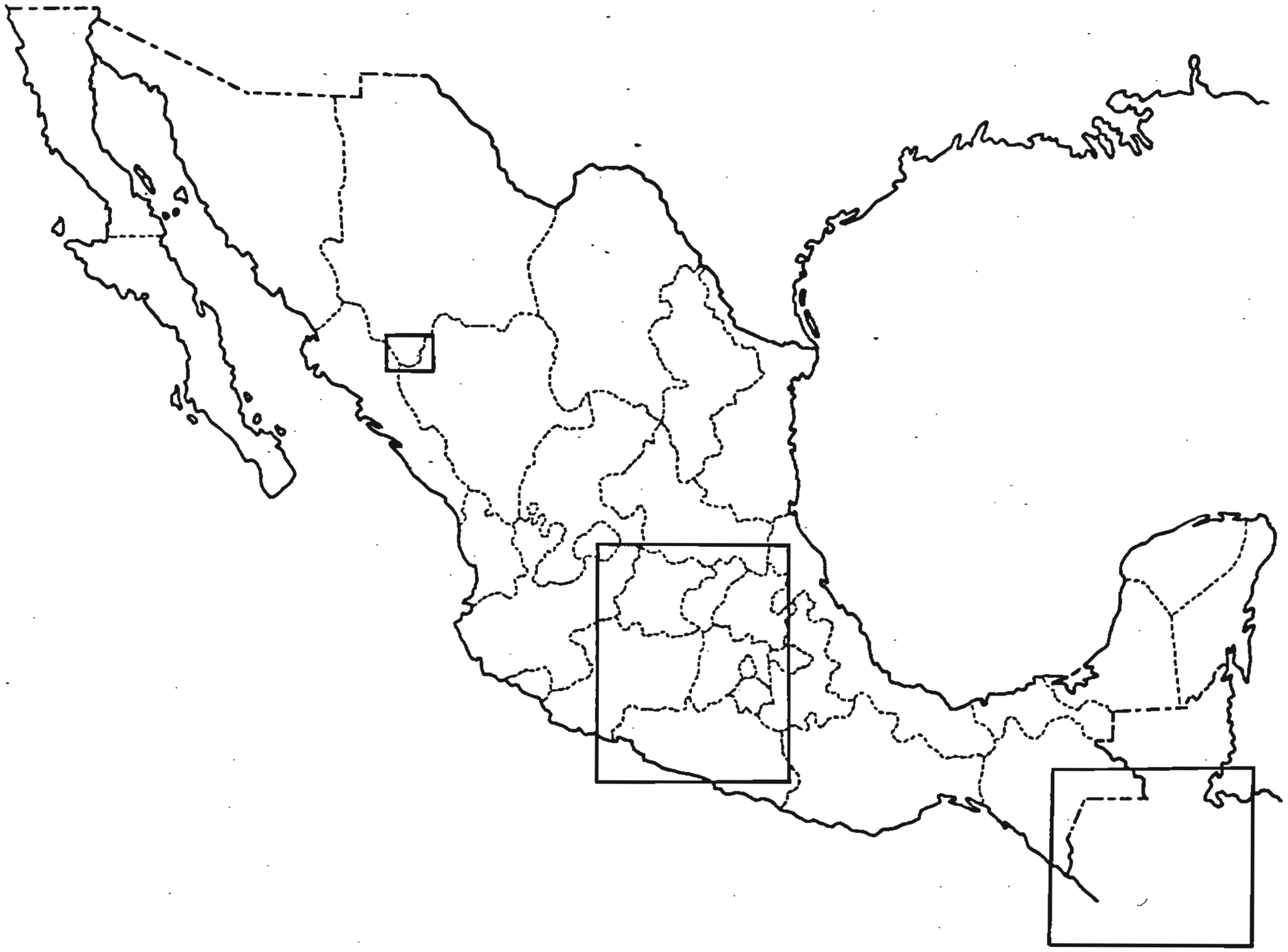

FIGURE 1. Map of Mexico showing the location of the regions concerned in the present studies.

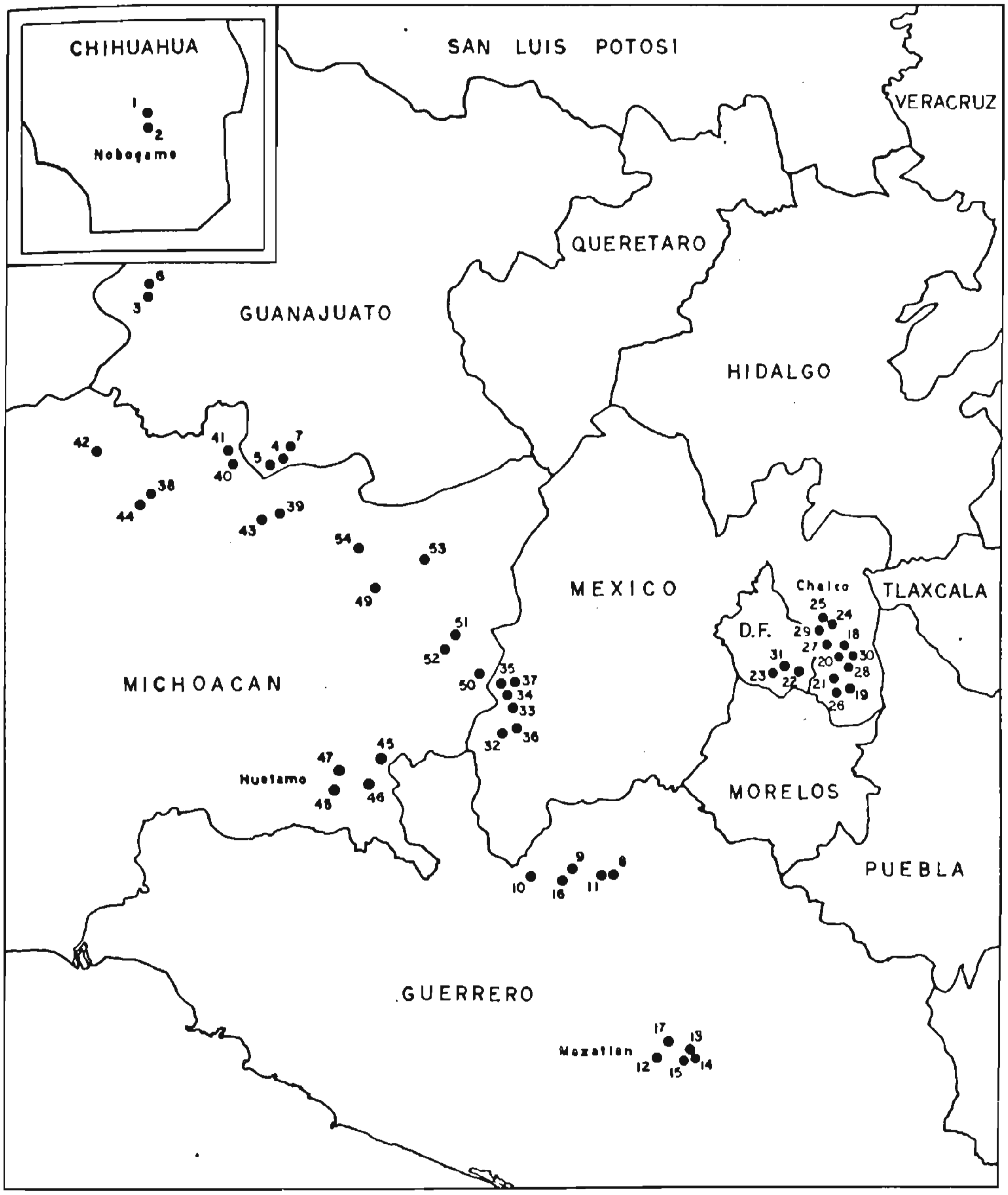

FIGURE 2. Geographical distribution of teosinte collections from Mexico according to their original collection places. The numbers correspond to the entries given in Appendix Table 1.

FIGURE 3. Geographical distribution of teosinte collections from Guatemala according to their original collection places. The numbers correspond to the entries given in Appendix Table 1.

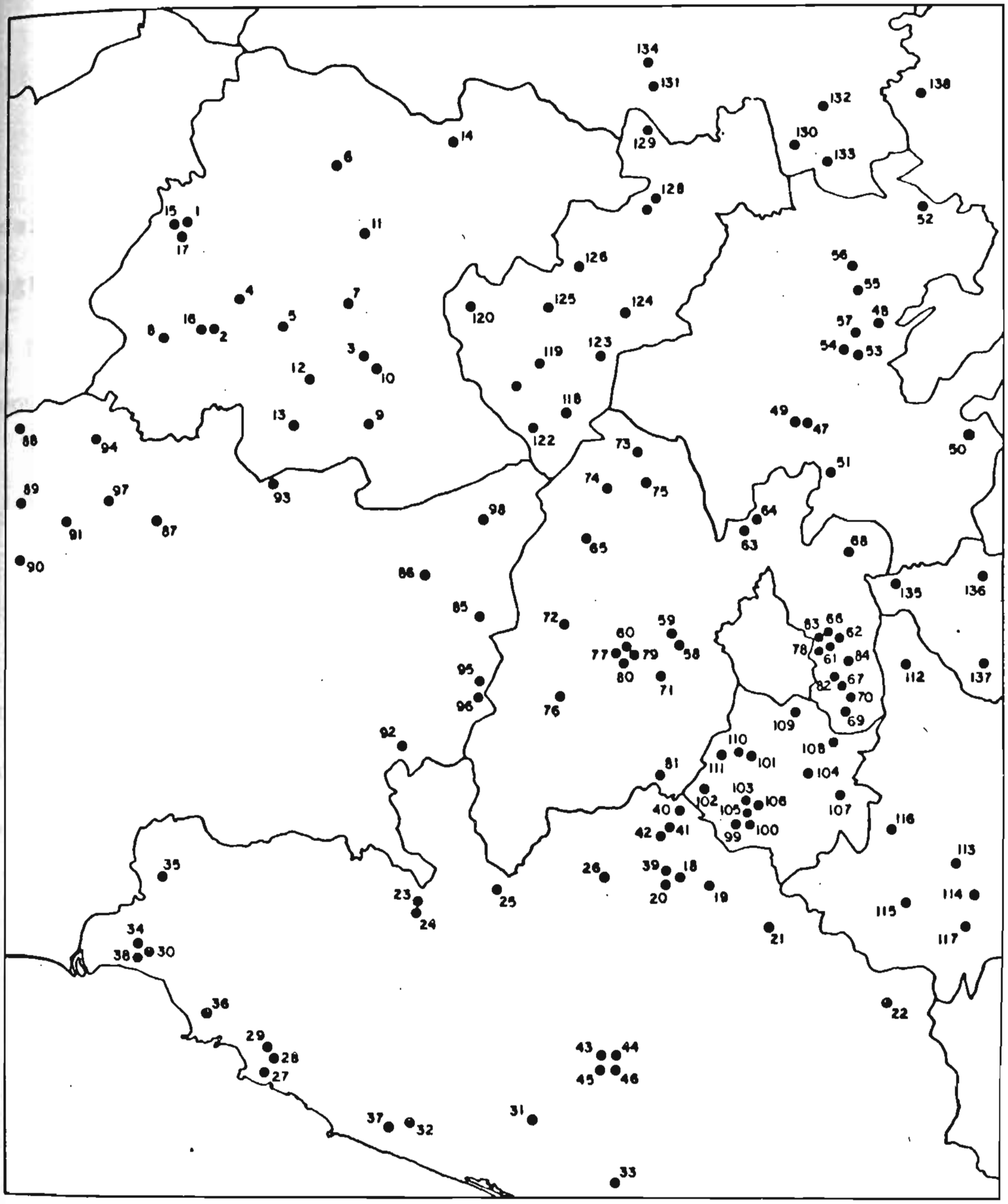

FIGURE 4. Geographical distribution of maize collections from central Mexico according to their original collection places. The numbers correspond to the entries given in Appendix Table 2.

CHAPTER IV

RESULTS

Chromosome Morphology

The chromosome morphology of the pachytene chromosomes of maize and teosinte can be studied from three different aspects: 1] the chromosome length and the arm ratio; 2] the chromomere distribution pattern; and 3] the presence or absence of knobs at the different positions on the chromosomes and their variation in size.

The results of a comparative study of pachytene chromosomes of maize and teosinte follow.

Chromosome length and arm ratio. The mean total length [in microns] of the ten chromosomes at the pachytene stage for each of the maize and teosinte plants used in this study is given in Text Table 2. These data show that statistically significant differences sometimes occur in the average total length when the same chromosome is compared between different plants of either maize or teosinte. For example, chromosome 1 of maize MZ-1 plant having an average length of 93.84 µ is significantly longer than chromosome 1 of both MZ-2 and MZ-3 which measured 81.24 µ and 79.26 µ respectively. The average length of the same chromosome 1 is longer in a teosinte TC-3 plant when compared with TC-1 and the difference is significant at the 1% level. Chromosome 1 of TC-3, however, is not different from that of TC-2 and TC-4. Furthermore, chromosome 1 of MZ-1 is significantly longer than the same chromosome of TC-1 but not different from that on any of the other teosinte plants.

The kind of relationships, as given above among the seven plants studied, are not apparent when the 10 chromosomes are considered independently of their genome. However, when the mean lengths for each chromosome are arranged in a descending order according to their source, as presented in Text Table 4, a significant difference becomes apparent because a pattern is revealed. In this new arrangement, it can be observed that almost all of the 10 chromosomes in the genome of TC-1 are shorter than their homologs in the other six plants. This permits a valid comparison of the mean lengths of all chromosomes of the other six plants with those of TC-1. That is to say, TC-1 can serve as an adequate baseline. The chromosomes of the plants MZ-1, TC-2, and TC-3 are always significantly longer than those of TC-1, with the exception of the cases of chromosome 6 in which only MZ-1 showed a significative difference, and of chromosome 8 in which TC-3 showed no significant difference from TC-1. However, these two extreme plants, MZ-1, TC-2, and TC-3 with the longest chromosomes, and TC-1 with the shortest ones, are bridged by the rest of the plants which have some chromosomes as long as those of the longest chromosome group and other chromosomes are equally short as those of the TC-1 plant, therefore showing an intermediate condition regarding this chromosome character. Furthermore, it is of interest to note that both maize and teosinte are represented in all of the chromosome groups.

These results clearly indicate that the length of the chromosomes is a character that does not demark the species although differences at the racial level may exist. How much this chromosome character depends either upon the genotype and/or the environmental factors is not evaluated in this study.

The mean arm ratio values and their standard deviations for each chromosome of the plants studied are given in Text Table 3.

TABLE 2. The mean total length [μ] values and their standard deviations for each of the ten chromosomes measured at pachytene stage of the maize and teosinte plants selected for this purpose.* Tukey's w values at .05 and .01 probability levels are given for each chromosome to show the statistical significance of the differences shown between any two of the means.

PLANT	CHROMOSOME				
	1	2	3	4	5
MAIZE					
MZ-1	93.84 ± 13.60	72.39 ± 8.17	69.57 ± 11.36	65.56 ± 5.47	72.95 ± 9.86
MZ-2	81.24 ± 7.78	68.56 ± 7.72	61.29 ± 6.53	59.35 ± 9.17	66.77 ± 5.55
MZ-3	79.26 ± 7.55	62.18 ± 5.35	58.82 ± 4.03	57.99 ± 5.16	60.75 ± 5.34
TEOSINTE					
TC-1	73.70 ± 8.63	52.92 ± 6.67	52.86 ± 6.56	50.94 ± 4.95	54.29 ± 6.30
TC-2	88.84 ± 4.89	74.52 ± 7.54	64.13 ± 7.36	61.30 ± 5.12	64.55 ± 6.29
TC-3	90.03 ± 9.54	69.79 ± 7.21	70.01 ± 6.51	64.88 ± 6.04	68.11 ± 9.40
TC-4	82.53 ± 9.97	61.04 ± 8.28	60.78 ± 12.05	54.65 ± 8.31	61.59 ± 8.48
TUKEY'S					
w[.05]	12.53	10.00	11.20	8.88	10.25
w[.01]	14.91	11.85	13.33	10.57	12.20

TABLE 2 [continued].

PLANT	CHROMOSOME				
	6	7	8	9	10
MAIZE					
MZ-1	52.05 ± 8.17	51.92 ± 8.61	53.09 ± 6.71	47.56 ± 5.34	40.58 ± 3.98
MZ-2	46.76 ± 4.45	46.48 ± 4.43	47.34 ± 8.07	39.55 ± 3.92	35.26 ± 3.53
MZ-3	44.93 ± 5.10	45.03 ± 4.01	45.34 ± 4.53	40.06 ± 5.00	35.31 ± 2.48
TEOSINTE					
TC-1	42.89 ± 3.97	39.05 ± 3.69	41.04 ± 3.61	35.79 ± 3.20	30.72 ± 3.45
TC-2	47.57 ± 5.89	49.12 ± 5.35	49.75 ± 3.25	45.48 ± 4.09	39.30 ± 3.65
TC-3	45.33 ± 5.56	47.91 ± 6.46	46.85 ± 8.43	48.99 ± 5.89	42.19 ± 3.33
TC-4	46.35 ± 8.23	46.01 ± 6.96	44.86 ± 6.09	43.56 ± 5.89	34.07 ± 2.78
TUKEY'S					
w[.05]	8.34	8.02	8.35	6.62	4.57
w[.01]	9.92	9.54	9.93	7.88	5.43

* MAIZE: MZ-1 Ozumba, Mexico
MZ-2 El Salado, Guerrero
MZ-3 El Salado, Guerrero

TEOSINTE: TC-1 Los Espinos, Michoacan
TC-2 Nobogame, Chihuahua
TC-3 Southern Guatemala
TC-4 Northern Guatemala

TABLE 3. The mean arm ratio [L/S] values and their standard deviations for each of the ten chromosomes measured at pachytene stage of the maize and teosinte plants selected for this purpose. Tukey's w values at .05 and .01 probability levels are given for each chromosome to show the statistical significance of the differences shown between any two of the means.

PLANT	CHROMOSOME				
	1	2	3	4	5
MAIZE					
MZ-1	1.40 ± 0.27	1.38 ± 0.19	2.05 ± 0.24	1.67 ± 0.13	1.03 ± 0.12
MZ-2	1.26 ± 0.13	1.32 ± 0.13	1.94 ± 0.25	1.85 ± 0.39	1.11 ± 0.01
MZ-3	1.30 ± 0.17	1.35 ± 0.14	2.10 ± 0.14	1.73 ± 0.14	1.06 ± 0.12
TEOSINTE					
TC-1	1.36 ± 0.07	1.35 ± 0.12	2.00 ± 0.23	1.78 ± 0.30	1.15 ± 0.10
TC-2	1.35 ± 0.11	1.28 ± 0.23	2.11 ± 0.21	1.58 ± 0.30	1.07 ± 0.14
TC-3	1.36 ± 0.20	1.32 ± 0.29	1.86 ± 0.28	1.94 ± 0.36	1.06 ± 0.17
TC-4	1.31 ± 0.14	1.44 ± 0.21	2.20 ± 0.34	1.48 ± 0.31	1.11 ± 0.18
TUKEY'S					
w[.05]	0.23	0.27	0.34	0.40	0.19
w[.01]	0.27	0.32	0.41	0.47	0.22

TABLE 3 [continued].

PLANT	CHROMOSOME				
	6	7	8	9	10
MAIZE					
MZ-1	3.61 ± 0.70	2.63 ± 0.34	3.37 ± 0.52	1.93 ± 0.36	2.46 ± 0.31
MZ-2	3.48 ± 0.67	2.96 ± 0.48	3.11 ± 0.54	2.16 ± 0.27	2.69 ± 0.40
MZ-3	3.74 ± 0.59	2.97 ± 0.23	3.39 ± 0.21	2.13 ± 0.24	2.49 ± 0.29
TEOSINTE					
TC-1	4.02 ± 0.66	2.54 ± 0.22	3.15 ± 0.45	1.98 ± 0.19	2.82 ± 0.57
TC-2	4.01 ± 0.84	2.42 ± 0.34	2.90 ± 0.23	2.21 ± 0.47	2.67 ± 0.26
TC-3	3.56 ± 0.61	2.89 ± 0.53	3.39 ± 0.63	2.75 ± 0.80	3.39 ± 0.49
TC-4	3.69 ± 0.90	2.52 ± 0.31	2.88 ± 0.42	2.13 ± 0.40	2.47 ± 0.40
TUKEY'S					
w[.05]	0.98	0.50	0.62	0.59	0.54
w[.01]	1.17	0.60	0.74	0.70	0.65

TABLE 4. Arrangement in a descending order of the three maize and the four teosinte plants used for pachytene chromosome measurements according to the mean total length values given in Table 2 for each of the 10 chromosomes of the complement.

Order	CHROMOSOME									
	1	2	3	4	5	6	7	8	9	10
1	MZ-1	TC-2	TC-3	MZ-1	MZ-1	MZ-1	MZ-1	MZ-1	TC-3	TC-3
2	TC-3	MZ-1	MZ-1	TC-3	TC-3	TC-2	TC-2	TC-2	MZ-1	MZ-1
3	TC-2	TC-3	TC-2	TC-2	MZ-2	MZ-2	TC-3	MZ-2	TC-2	TC-2
4	TC-4	MZ-2	MZ-2	MZ-2	TC-2	TC-4	MZ-2	TC-3	TC-4	MZ-3
5	MZ-2	MZ-3	TC-4	MZ-3	TC-4	TC-3	TC-4	MZ-3	MZ-3	MZ-2
6	MZ-3	TC-4	MZ-3	TC-4	MZ-3	MZ-3	MZ-3	TC-4	MZ-2	TC-4
7	TC-1	TC-1	TC-1	TC-1	TC-1	TC-1	TC-1	TC-1	TC-1	TC-1

TABLE 5. Arrangement in a descending order of the three maize and the four teosinte plants used for pachytene chromosome measurements according to the mean arm ratio values given in Table 3 for each of the 10 chromosomes of the complement.

Order	CHROMOSOME									
	1	2	3	4	5	6	7	8	9	10
1	MZ-1	TC-4	TC-4	TC-3	TC-1	TC-1	MZ-3	MZ-3	TC-3	TC-3
2	TC-1	MZ-1	TC-2	MZ-2	MZ-2	TC-2	MZ-2	TC-3	TC-2	TC-1
3	TC-3	MZ-3	MZ-3	TC-1	TC-4	MZ-3	TC-3	MZ-1	MZ-2	MZ-2
4	TC-2	TC-1	MZ-1	MZ-3	TC-2	TC-4	MZ-1	TC-1	MZ-3	TC-2
5	TC-4	MZ-2	TC-1	MZ-1	MZ-3	MZ-1	TC-1	MZ-2	TC-4	MZ-3
6	MZ-3	TC-3	MZ-2	TC-2	TC-3	TC-3	TC-4	TC-2	TC-1	TC-4
7	MZ-2	TC-2	TC-3	TC-4	MZ-1	MZ-2	TC-2	TC-4	MZ-1	MZ-1

The data in Text Table 3 show that, with a few exceptions, there are no statistically significant differences between the mean arm ratios of the 10 chromosomes in the plants of maize and teosinte studied. In those few cases where significant differences were found, they occurred between plants having only the extreme mean values. Even here, the range in the variability of these extreme values overlap in a large extent.

When plants are arranged in a descending order according to the mean arm ratio values for each of the 10 chromosomes, the resultant arrangement is that given in Text Table 5. From this table, it is clear that the relative position of any plant within the arrangement is at random, without showing any apparent pattern.

These results lead to the conclusion that the arm ratio of any particular chromosome of the complement is very constant and there is no difference whether it is obtained from different plants of either maize or teosinte.

When the results of both the chromosome length and the arm ratio studies are considered together, the general conclusion is inescapable that the average value of the arm ratio of any chromosome is fairly constant and does not depend upon the length that the chromosome can attain, which is variable depending on the genetic and/or environmental factors acting on it. This means, therefore, that the chromosomes can reach the pachytene stage of microsporogenesis, and probably also of megasporogenesis, with different average lengths, but always the relative lengths of their long arms with respect to the corresponding short arms remain constant. Finally, both chromosome characters, length and arm ratio, do not show any difference between maize and teosinte at the species level, although some indication has been obtained that the chromosome length might be race and/or variety specific.

Chromomere distribution pattern. The chromomere distribution pattern refers to conspicuous single chromomere or series of chromomeres that can be observed in different regions of the pachytene chromosomes. Each chromosome of the complement has a very characteristic linear arrangement of chromomeres. However, the conspicuousness of the chromomeres vary mainly because chromosomes of different plants of a variety, or of plants of different varieties, do not have the same ability to become well stained and also because the chromomeres show variation in size. This kind of variation, however, is not specific to either maize or teosinte.

The general characteristics used for identifying the pachytene chromosomes of maize are also useful with teosinte. These characteristics are the relative chromosome lengths, the chromosome arm ratios, the patterns of conspicuous chromomeres, and the distribution of knobs. Since the presence of the knobs is variable, as will be shown later on, and because there exist many knobless or almost knobless populations of maize and teosinte, and also because many populations possess more than one knobless chromosome, it seems appropriate to designate as one type of "basic chromosome morphology" that of the completely knobless complement. It is improbable, however, that this type of complement was the original one for either maize or teosinte.

A very general description of the most salient characteristics of the chromomere patterns of the knobless chromosomes follow. Plates I, II and III of the pachytene chromosomes of maize, and of Mexican and Guatemalan teosintes show some of these chromomere characteristics. Their descriptions reveal the close similarity of these chromosomes between these two plant species, not only in their size, but also in their basic chromosome organization at the optical level.

Chromosome 1 in its knobless condition does not have any conspicuous chromomeres, but the proximal segment on the short arm usually is darker than the proximal segment on the long arm side. This feature, plus the fact that it is the longest chromosome of the complement, makes it relatively easy to be identified. Plate I, Figure 1 and 2 show the general similarity of this chromosome in maize and Mexican teosinte.

Chromosome 2 commonly is confused with chromosome 5 but, besides the different arm ratios, there are some features that make them easy to be distinguished one from the other. Chromosome 2 has proximal segments of approximately equal length of heterochromatic nature while the corresponding segments in chromosome 5 differ in darkness, the segment on the short arm generally is lighter than the one on the long arm. Also, the most distal segment of the long arm of chromosome 2 usually possesses a unique series of conspicuous chromomeres. These chromomeres are not only absent in chromosome 5, but also they do not occur in any similar pattern in the other chromosomes [Figures 3, 4, and 5 of Plate I].

The short arms of chromosomes 3 and 4, in many cases show some similarity in length and in darkness of the centromeric heterochromatic segment. However, when well stained, it seems that chromosome 4 possesses larger and darker heterochromatic segments than chromosome 3. Furthermore, at a distal subterminal position of the short arm, chromosome 4 frequently shows a very distinct chromomere which in most of the cases is the best feature for distinguishing this chromosome arm from the others [McClintock, 1933]. In plants of Chalco teosinte, this position is frequently occupied by a small or medium size knob. On the other hand, the long arms of these chromosomes are completely different and, in most cases, they are distinguished easily. The long arm of chromosome 3 frequently has a large chromomere near its center [Rhoades and Dempsey, 1953]. Instead of the chromomere, a small or a medium size knob has been observed in a few plants of some collections of Mexican teosinte. The long arm of chromosome 4 is characteristically marked with a segment of about one fourth of its length that is darkened by large chromomeres. The $4L_1$ knob position is located in the middle of this segment [Figures 8, 9, and 10 of Plate I].

Chromosome 6 is the most easily identified chromosome of the complement because the nucleolar organizer in its short arm is always attached to the nucleolus. Very frequently the long arm shows a large chromomere in a similar position as the one in the long arm of chromosome 3. The similarity of this chromosome in maize and teosinte is shown in Plate II, Figures 11, 12, and 13.

There is a short and thick proximal heterochromatic segment on the long arm side which is characteristic of chromosome 7 in both maize and the teosintes of Mexico and Guatemala. In most of the cases where knobs are absent, this single feature is the most useful in distinguishing chromosome 7 from chromosome 8 [Longley, 1938; compare Figures 14-17 and Figures 18-21 of Plate II].

Chromosome 9 is characterized by segments of heterochromatic nature similar in length and darkness on both sides of the centromere. This feature combined with the fact that the short arm of chromosome 9 is the longest of the 5 shorter chromosomes of the complement makes it easy to identify. The characteristics of this chromosome are shown in Figures 22 to 24 of Plate III.

Finally, chromosome 10 has two characteristic groups of chromomeres. One is proximal on the short arm which is rather a thick heterochromatic segment occupying almost half the length of the short arm. The proximal segment of the long arm usually is not of heterochromatic nature. The second characteristic segment is located in the middle of the long arm having a length of about one third of the long arm and comprises a series of conspicuous chromomeres that give the segment a darker aspect with respect to the adjacent segments. This chromomere pattern of chromosome 10 is generally well developed in maize and in the teosintes from Mexico and northern Guatemala, but it seems less distinct in southern Guatemala teosinte as shown in Figures 25 to 28 of Plate III.

The above description of the pachytene chromosomes clearly indicates that there are so many identical chromosome segments between maize and both the Mexican and the Guatemalan teosintes that the conclusion stating that these plant species have the same chromosome complements is further substantiated.

Knob position and size. Chromosome knobs have been found at many different positions on the chromosomes of both maize and teosinte, forming highly polymorphic populations in regard to the wide range of combinations of several knob sizes.

The knobbed positions found in the maize collections studied are

TABLE 6. Overall frequencies of the various knob sizes [l,m,s,o] found at the different knob positions of the chromosomes of maize and Mexican teosinte. The knob positions are those given in Text Figures 5A and B.

Knob Posit.	MEXICAN TEOSINTE				TOTAL NO. CHROM.	M A I Z E				TOTAL NO. CHROM.
	Knob Size					Knob Size				
	l	m	s	o		l	m	s	o	
$1S_2$	206	99	19	296	620	310	333	100	821	1564
$1S_1$	2	2	3	613	"	-	-	-	-	"
$1L_1$	214	48	36	322	"	49	53	28	1434	"
$1L_2$	-	-	94	526	"	-	-	-	-	"
$2S_2$	1	-	2	617	"	-	-	-	-	"
$2S_1$	265	78	28	249	"	285	78	38	1159	1560
2L	311	33	10	266	"	546	213	25	776	"
$3S_2$	-	4	28	588	"	-	-	-	-	1564
$3S_1$	71	63	5	481	"	35	48	3	1478	"
3Lo	-	-	4	616	"	-	-	-	-	"
$3L_1$	236	67	6	311	"	578	246	24	716	"
$3L_2$	-	2	19	599	"	-	-	-	-	"
$4S_2$	58	49	23	490	"	3	4	1	1550	1558
$4S_1$	-	1	31	588	"	-	-	-	-	"
$4L_1$	379	66	20	155	"	979	201	26	352	"
$4L_2$	-	1	-	619	"	-	-	-	-	"
$5S_2$	-	1	-	619	"	-	-	-	-	1560
$5S_1$	78	22	1	519	"	9	3	1	1547	"
$5L_1$	450	52	2	116	"	1015	211	70	264	"
$6L_1$	152	23	3	442	"	26	138	56	1342	1562
$6L_2$	1	17	217	385	"	-	10	369	1183	"
$6L_3$	94	76	85	365	"	38	174	378	972	"
$6L_4$	-	2	8	610	"	-	-	-	-	"
7S	76	62	23	459	"	2	29	10	1523	1564
$7L_1$	332	57	6	225	"	817	263	49	435	"
$7L_2$	-	4	65	551	"	-	-	-	-	"
8S	-	5	38	577	"	-	-	-	-	1562
$8L_1$	307	72	9	232	"	478	362	42	680	"
$8L_2$	-	10	197	413	"	-	-	233	1329	"
9S	273	57	36	254	"	637	172	73	682	1564
$9L_1$	-	-	16	604	"	-	-	-	-	"
$9L_2$	26	35	17	542	"	42	102	33	1387	"
$10L_1$	-	30	11	579	"	-	1	-	1563	"
$10L_2$	-	8	40	572	"	-	14	105	1445	"

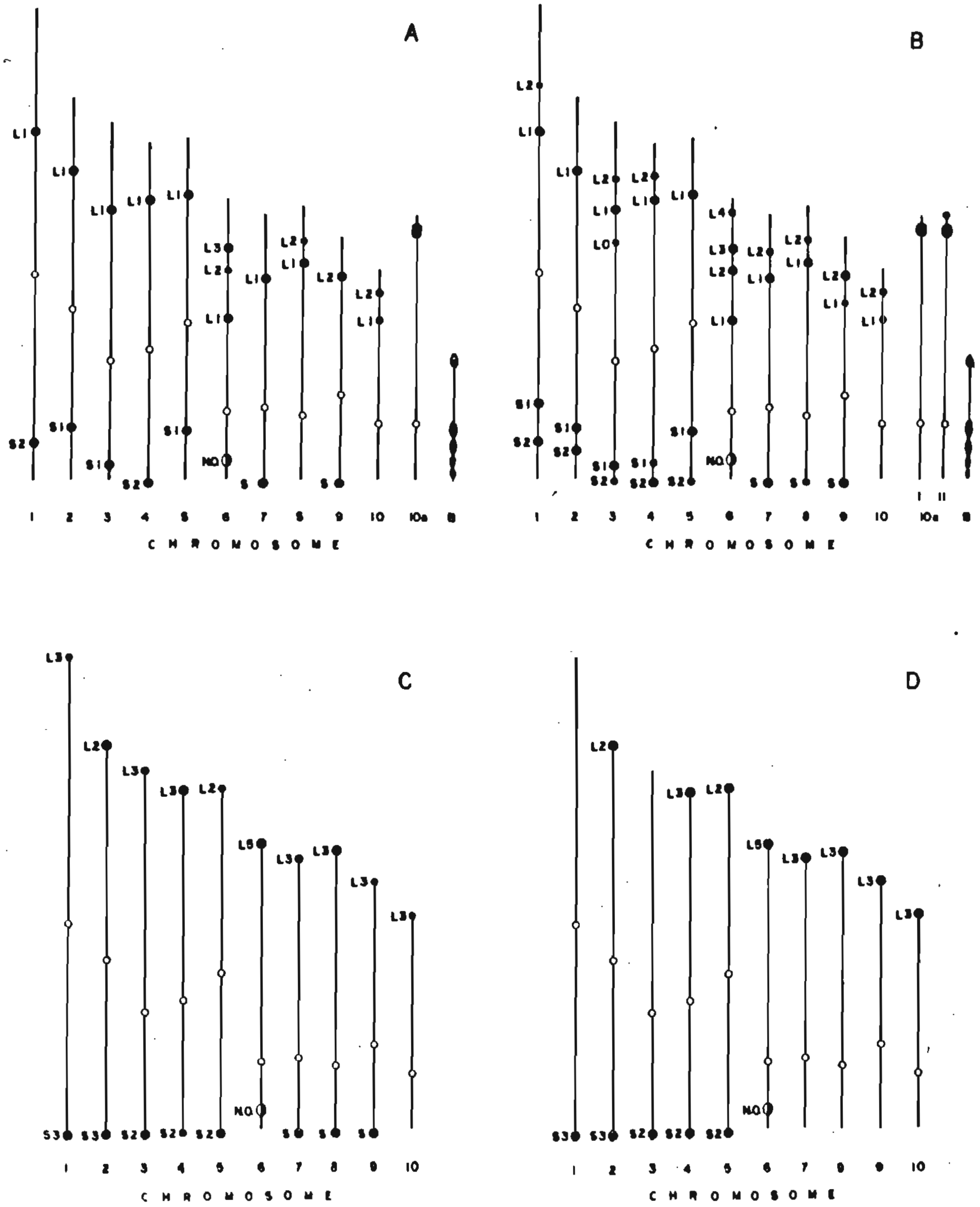

FIGURE 5. Idiograms of pachytene chromosomes of: A. Maize; B. Mexican teosinte; C. Northern Guatemala teosinte; and D. Southern Guatemala teosinte. The knob positions [black circles] and their designations are given as used in the present studies. Centromeres are represented by open circles and the nucleolar organizer by N.O.

given in the idiogram of Text Figure 5A. A total of 21 positions are given without including the large knob of the abnormal chromosome 10. Actually 22 positions are known according to the literature. The terminal knob position on the short arm of chromosome 1 has not been included in the idiogram of Figure 5 because no knob was found at this position in the collections examined for the present study.

The knobbed positions found in the collections of Mexican teosintes are given in the idiogram of Text Figure 5B. A total of 34 positions are represented, disregarding those knobs of the two types of abnormal chromosome 10. This number of knob positions certainly is much higher than the 21 already reported in the literature.

When Text Figure 5A is compared with Text Figure 5B, it is clear that maize populations possess less knobbed positions than Mexican teosinte populations. Also the positions showing knobs in maize have the exact counterparts in the chromosomes of the Mexican teosinte.

Text Table 6 presents the frequencies in which the knobs of different sizes were found at each of the positions of the maize and the Mexican teosinte chromosomes, as shown in Text Figures 5A and 5B. These frequencies are in terms of the total number of each of the maize and teosinte chromosomes examined in the present study. The data in this table show, in the first place, that most of the common knobbed positions between maize and Mexican teosinte also show similar relative frequencies in both plant species. Moreover, it can also be noticed in the data of Text Table 6 that those positions at which knobs were found only in teosinte, the frequencies for these knobs are in general low or very low, and these knobs tend to be of small size.

There is one further interesting fact that can be observed in Text Table 6, namely that when 2 or more knob positions exist on the same chromosome arm, only one of them shows predominance for the large knob size, while the other tends to have the small knob size. This situation is found between the positions $1S_1$ and $1S_2$; $1L_1$ and $1L_2$; $2S_1$ and $2S_2$; $3S_1$ and $3S_2$; 3Lo, $3L_1$, and $3L_2$; $4S_1$ and $4S_2$; $6L_1$, $6L_2$, $6L_3$, and $6L_4$; $7L_1$ and $7L_2$; $8L_1$ and $8L_2$; $9L_1$ and $9L_2$; and finally $10L_1$ and $10L_2$; almost in every chromosome of the complement. An exception occurs on chromosome 6 in the $6L_3$ position where all three knob sizes were found in similar frequencies. A clearer picture of this exceptional case can be observed when a geographical distribution of the collections having these knobs are examined, as will be given in a later chapter.

The positions in which knobs were found in Guatemalan teosinte are given in the idiograms of Text Figures 5C and 5D. The difference is striking when these two idiograms are compared to those of Mexican teosinte and of maize given in Text Figures 5A and 5B. The Guatemalan teosintes have shown only terminal knobs, both on the long and the short arms, while in maize and Mexican teosinte, most of the knobs are in intercalary positions. The terminal knobs on the long arms and those on the short arms of chromosomes 1 and 2 of Guatemalan teosintes were not observed in any plant of maize nor of Mexican teosinte populations examined. Nevertheless, there are several knobbed positions in common between Guatemalan and Mexican teosintes with those of maize. The positions $3S_2$, $4S_2$, $5S_2$, 7S, 8S, and 9S have shown knobs in Guatemalan and Mexican teosintes, while the positions $4S_2$, 7S, and 9S were found having knobs in maize and in both the Mexican and the Guatemalan teosintes.

Interestingly, most of the differences between the chromosomes of northern and southern Guatemala teosintes were found in the four shortest chromosomes of the complement. The northern Guatemalan teosintes had knobbed short arms of chromosomes 7, 8 and 9, whereas the long arms were mostly knobless, and the knobs present were of small size in most cases. The short arm of chromosome 10 appeared to be knobless in teosintes of both Guatemalan regions. On the other hand, the southern Guatemala teosinte possessed only knobless short arms of chromosomes 7, 8 and 9, while their long arms showed knobs of different sizes with a preponderance of the large ones. However, it is clear that always the knobless positions were present, as also was the case for all the other chromosomes.

Among the long chromosomes, the long arm of chromosome 3 was knobless in the southern Guatemala teosinte while the northern ones possessed medium and small knobs. Also the long arm of chromosome 1 was knobbed with a small size knob only in one plant from northern Guatemala, so that practically all the teosintes of both regions were the same in regard to this particular position.

In summary, from the above account of the knobs found in maize, and the Mexican and Guatemalan teosintes, it can be concluded that, in general, these populations were found to have different knob constitutions. Mexican teosintes have more positions showing knobs than maize, but many of these positions were common to both and they have knobs in similar over-all frequencies. Also those knobbed positions found only in teosinte tend to carry only small knobs in very low frequencies. Contrary to this situation, Guatemalan teosintes are different in that they possess exclusively terminal knobs. However, the differences separating maize and Mexican teosinte from Guatemalan teosintes are not absolute since several knobs are present in common positions, and more important, because all knob positions in all populations of maize and teosinte show the knobless condition in various frequencies.

Knob Distribution in Teosinte

Mexican teosinte. The geographical distribution of the relative frequencies of the several knob types found in teosinte collections from Mexico has revealed that the knobs at different positions show several distinct distribution patterns.

There is one group of general knob positions [$1S_2$, $2S_1$, $2L_1$, $3\ L_1$, $4L_1$, $5L_1$, $7L_1$, $8L_1$, and 9S] found in populations from most of the regions under study [Appendix Figures 1, 4, 6, 8, and 14]. This group usually has either a large knob or it is knobless in each position although the relative frequencies of each of these conditions are not uniform in all the regions. The medium and small knobs were only present in low frequencies. The small knobs had the lowest frequencies and in most of the collections studied this type was absent. In one extreme case in the $5L_1$ position, there were no small knobs in any of the collections from central Mexico, and only one of the collections from Nobogame showed it in a low frequency [2 out of 26 chromosomes]. One of the regions that was consistent is Chalco, where the large knobs in most positions of the group were found in high frequencies and consequently the knobless positions were relatively less frequent. In this regard, the 9S position was the exception as will be shown later on. The predominance of the large knobs were found in all the regions in the cases of $4L_1$ and $5L_1$ positions, with the exception of the collections from Nobogame where the $4L_1$ position was predominated by small knobs and the knobless condition, and the $5L_1$ position by the knobless condition [Appendix Figures 6 and 8].

The $3L_1$ position has shown some regional differences regarding the frequencies of its knob types, especially the large knobbed and the knobless conditions [Appendix Figure 4]. As already mentioned, in the Chalco region, the large knobs showed a high frequency while the knobless segments were present in rather low frequency. On the other hand, those regions located between the limits of southeastern Michoacan and central Guerrero have shown populations with a situation which is the opposite of that of the Chalco region, that is, the knobless condition was prevalent while the large knobs tended to be present in low frequencies. This situation was more clearly shown by populations of the S.E. Michoacan-W. Mexico region. The Guanajuato-N. Michoacan region in general had most of its populations more similar to those of the Chalco region, although few of the former populations were of the S.E. Michoacan-W. Mexico type, therefore showing a kind of mixed condition.

Contrary to the above situation, the 9S position showed that in populations of the Chalco region the large knobs and the knobless positions were both more frequent than the medium and the small knobs [Appendix Figure 14]. Also the other regions had populations showing the reverse situation when compared to the knob frequency distribution of the $3L_1$ position. Namely, the populations of the Guanajuato-N. Michoacan region were predominated by knobless 9S position, whereas in more southern regions toward central Guerrero, the large knobbed 9S positions were predominant. A similar situation to the 9S position was shown by the knobs in the $7L_1$

and $8L_1$ positions.

Further meaningful relationships have been observed when the knob distribution in the $3L_1$, $7L_1$, and 9S positions were compared with that of other positions located on the same chromosome, that is $3L_1$ with $3L_2$, $3S_1$ and $3S_2$ [Appendix Figures 3 and 4], $7L_1$ with $7L_2$ and 7S and 9S with $9L_1$ and $9L_2$ positions [Appendix Figures 14, 15, and 16].

In the case of the $3S_1$ position, the populations of the Chalco region are largely knobless since the knobs present were of medium size [except one chromosome which had a large knob] and in rather low frequencies. In regard to other regions, most of the knobs found were of large and medium size and also the majority of the populations having these knobs were located in the regions of S.E. Michoacan, W. Mexico and Guerrero, while only a few of these populations were from Guanajuato-N. Michoacan region. The $3S_2$ and the $3L_2$ positions were found possessing knobs of medium and small knobs in rather low frequencies. Nevertheless, the general distribution pattern is similar to that of the $3S_1$ position. This pattern, shown by the $3S_1$, $3S_2$, and $3L_2$ positions, is the reverse situation to that shown by the knobs at the $3L_1$ position.

The knobs found at the $9L_1$ position were only of the small size in low frequencies, and also found only in few scattered populations of the Guanajuato-N. Michoacan regions [Appendix Figure 15]. The $9L_2$ position, on the other hand, possessed low frequencies of the large, medium, and small knobs in general following the same distribution of the $9L_1$ small knobs [Appendix Figure 16]. However, several populations having knobs at the $9L_2$ position were found in regions of S.E. Michoacan, W. Mexico and Guerrero, but in relatively lower frequencies than in more northern regions.

It seems, therefore, that the frequency distribution of knobs at the 9S position tend to show a reverse situation to that shown by the knobs at the $9L_1$ and $9L_2$ positions. In other words, when 9S position showed high knob frequencies in a given region, the $9L_1$ and $9L_2$ position had no knob at all or had knobs in relatively low frequencies and, when the knob frequencies at the 9S position were lowered, it seems that the knob frequencies for the $9L_1$ and $9L_2$ tended to be increased accordingly.

When the frequency distribution of the different knob types of the $7L_1$ position was compared with that shown by the 7S position, it was found that the relative knob frequencies of the $7L_1$ position was high in a given region, while the knob frequencies of the 7S position tended to be relatively lower in populations of the same region. For example, at the $7L_1$ position in Guerrero, the knobs, especially the large ones, were found in a high frequency, while the knobs at the 7S position were present in a low frequency in the same populations. A similar situation was observed in Guanajuato-N. Michoacan regions. In other cases, such as in E. Michoacan-W. Mexico regions, knobs at both positions have shown higher frequencies than in the regions to the north and to the south. In the Chalco region, the $7L_1$ position has shown large knobs in high frequencies with the other knob types being present in low frequencies, whereas at the 7S position different knob types were found in lower frequencies but forming a more balanced polymorphism [Appendix Figure 12].

The $7L_2$ position has presented mostly small knobs with the exception of a single collection from Huetamo in southeastern Michoacan that showed some medium size knobs. Even though these knobs were found in rather low frequencies and distributed among populations of the regions from Guanajuato-N. Michoacan, S.E. Michoacan-W. Mexico and Guerrero, it seems that they are relatively more frequent in the southern regions than in the northern ones of the distribution range. This distribution pattern, in general, seems to be similar to the distribution shown by the large knobs of the $7L_1$ position. However, they differ in that the knobs of the $7L_2$ position were absent from the Chalco region, while those of the $7L_1$ position were found in a very high frequency in this region.

There is a second group of knob positions [e.g., $1L_2$, $6L_2$, $8L_2$, $10L_1$ and $10L_2$] which is characterized by a general absence of large knobs. However, there was an exception in one plant of Nobogame that showed a single chromosome with a large knob in $6L_2$ position. Another general characteristic of this group of knob positions is that they were predominated by small knobbed and knobless conditions in the teosinte populations of all regions concerned in this study. The medium knobs were generally found at these positions, except at $1L_2$, in very low frequencies in scattered populations of various regions.

Two general distribution patterns were found among the knob positions of this group: a] one pattern is shown by the $1L_2$, $6L_2$ and $8L_2$ positions in populations of almost all the regions from central Guerrero through Guanajuato where these positions carry small knobs in relatively high frequencies when compared to the knobless positions, the other prevalent condition [Appendix Figure 10]. The main variations were found in Chalco and Nobogame populations. The $1L_2$ position was almost knobless in populations of both regions and only one chromosome out of 166 had a small knob. A similar situation was found for the $8L_2$ position. On the other hand, the $6L_2$ position tended to be more similar in populations of Chalco and Nobogame with those of the other regions; b] the second pattern concerns the knobs at the $10L_1$ and $10L_2$ positions. In this case the knobs were usually in very low frequencies and scattered in a few collections from each of the regions. Two exceptions were found. The medium knob at $10L_1$ position appeared to be somewhat more frequent in populations of the Guanajuato-N. Michoacan region, and the small knob at $10L_2$ was found in relatively high frequencies in populations of the Chalco region.

There is another pattern in which knob positions do not carry knobs in populations of one or more regions while knobs at the same positions occur, in many cases, in relatively high frequencies elsewhere. In the first example there are two knob positions, $1L_1$ and $6L_1$, with knobs that usually follow a distribution pattern similar to that shown by the knobs in the $3L_1$ position described above. That is, large knobs are present in high frequencies in the Chalco region and in the Guanajuato-N. Michoacan region, while they are less frequently found in populations of the regions comprised by S.E. Michoacan, W. Mexico and Guerrero. The major difference shown by the $1L_1$ and $6L_1$ positions with respect to the $3L_1$ position, however, lies in the S.E. Michoacan-W. Mexico-Guerrero region. The knobs are absent from the $1L_1$ position in populations of the northern portion, while low knob frequencies occur in the southern part of this general region. The knobs are also absent from the $6L_1$ position in populations of the whole major region. Another difference observed in the $6L_1$ position is that the knob frequencies found in populations of the Guanajuato-N. Michoacan region are lower than the frequencies found at $3L_1$ and $1L_1$ positions in the same region.

The terminal knob position on the short arm of chromosome 4 [$4S_2$] and the internal knob position on the short arm of chromosome 5 [$5S_1$] have shown a similar knob distribution [Appendix Figures 5 and 7]. In the Chalco region, the overall knob frequencies seem to be relatively high in comparison with the other regions. Also the large knobs are relatively more frequent than the medium knobs with the small knobs being the least frequent. The populations of the Huetamo region in southeastern Michoacan and those of Guerrero showed moderate frequencies of knobs at these positions. On the other hand, those populations of more northern regions located in southern Guanajuato and northern Michoacan were found to be almost knobless in relation to these positions.

The $4S_1$ position which is located subterminally and close to the $4S_2$ terminal position usually shows a conspicuous large chromomere that is characteristic and very useful for identifying the distal segment of the short arm of chromosome 4. However, plants of different collections of the Chalco region, and a single plant from western state of Mexico, have shown a distinct small knob at the $4S_1$ position. The frequency of this small knob was relatively high in the Chalco region, but with the exception mentioned, all the collections from regions of Guanajuato, Michoacan, western state of Mexico and Guerrero showed only the knobless condition at the $4S_1$ position.

The 8S position usually had small knobs and most of the populations having them were of the S.E. Michoacan, W. Mexico and Guerrero regions. The frequencies were, in general, low. The Guanajuato-N. Michoacan region showed only one small and one medium knob in two different collections. The Chalco region showed absence of these knobs [Appendix Figure 13]. Disregarding the Chalco region, the knob distribution of the 8S position seems to be similar to that of knobs found at the $3S_1$ position as described above.

It has been already shown in several chromosomes that the knob positions located on a given chromosome, especially between positions on the long and short arms, had knobs following reciprocal distribution patterns as if the absence of knobs from one of the positions was compensated by the presence of knobs in the other position. A similar situation is found when the knob frequency distribution of the $6L_1$, $6L_2$, $6L_3$, and $6L_4$ positions are considered [Appendix Figures 9, 10, and 11].

In the Chalco region the $6L_1$ position usually has large knobs, whereas the $6L_3$ position is usually knobless in populations of the same region. In the S.E. Michoacan, W. Mexico and Guerrero regions a reverse situation of the Chalco region is observed, in other words the $6L_1$ position is totally knobless while the $6L_3$ position, though not predominated by any of the knob types, the knobs seem to form a balanced polymorphic condition. On the other hand, in more northern regions of Guanajuato-N. Michoacan, this kind of relationship is less apparent with an intermediate condition of balanced polymorphism in the two positions. Nevertheless, there is a difference between the knob types found at these two positions. The $6L_1$ position showed only knobs of the large and medium sizes, while the $6L_3$ position possessed only knobs of medium and small sizes, that is, the former position tends to have larger knobs than the latter position although the frequencies are similar. Contrary to the distribution patterns shown by the $6L_1$ and $6L_3$ positions, the $6L_2$ position, which is located between the former two positions, is predominated by small knobs and the knobless position in populations of all the regions. The $6L_4$ position showed medium and small knobs in low frequencies and their distribution was found to be restricted to the populations of northern Guerrero.

In other cases, such as in chromosomes 4 and 5 of all regions that have shown high frequencies of knobs in the positions on their long arms, especially of the large size, the knob positions on their short arms also possess knobs in relatively high frequencies in certain regions, but absent in other regions [Appendix Figures 5, 6, 7, and 8]. In these cases, it seems that the presence of knobs on both arms of the chromosome are advantageous to the populations in some regions but not in others, and in this regard they might have a complementary effect rather than compensatory one as found in other cases described before.

In general, it is observed that when two or more knob positions exist in a single chromosome arm, usually only one [except chromosome 6] tends to show knobs in high frequency and of the larger size, while the other positions tend to be knobless or possess only small knobs. In many cases like the $1L_2$, $6L_2$, and $8L_2$ positions, the small knobs are present in high frequencies and with a wide distribution in populations of many regions, indicating that they might have some complementary effect to the major knob position located nearby in the same chromosome arm.

Guatemalan teosinte. The Guatemalan teosinte collections can be grouped into two sharply separated groups: the northern Guatemala group formed by those collections coming from the department of Juejuetenango, and the southern Guatemala group comprised by those collections made in the departments of Jutiapa and Chiquimula [Text Figure 3].

The comparative analysis of the knob frequency distribution of teosinte populations from the two Guatemalan regions has resulted in the finding of three major groups of knob positions showing three distinct distribution patterns. All the knob positions are terminally located and their designations are given in Text Figures 5C and 5D.

1. The first group is comprised by the $1S_3$, $1L_3$, $2S_3$, $3S_2$, $4L_3$, $5S_2$ and 10S terminal knob positions. The knobs at these positions were found in similar frequencies in collections from both Guatemalan regions, with some minor differences [Appendix Figures 30, 32, and 35]. One of the differences found is that the small knobs at the $1S_3$, $2S_3$, and $3S_2$ positions were absent in the collections of southern Guatemala while they were present in variable frequencies in the northern populations. Another difference regards the $4L_3$ position because, in southern Guatemala collections, the medium knobs showed a higher frequency than the large and small knobs and the knobless condition, while in the northern collections a more balanced condition of the different knob types was found. In the cases of $1L_3$, and 10S positions, a similarity is that the knobs were absent from these positions in both populations, with the exception of a single chromosome of a plant from Tzisbaj, Huejuetenango that showed a small knob at the $1L_3$ position.

2. The next group of knob positions is characterized by the fact that the distribution of the knobs at these positions was found to differ between the populations of northern and southern Guatemalan regions. This group comprises the $3L_3$, 7S, 8S and 9S positions. These knob positions possessed different knob types with variable frequencies, while the collections from the southern regions possessed no knob at these positions [Appendix Figures 33, 36, and 38]. In the particular case of $3L_3$ posi-

tion, no large knobs were found in the collections of northern Guatemala and the medium and small knobs were present in rather low frequencies. With the exception of the 7S position which showed similar higher frequencies of the large knobs and the knobless positions over the medium and small knobs, the 8S and 9S positions had predominantly large knobs.

3. The third group is formed by the $2L_2$, $4S_2$, $5L_2$, $6L_5$, $7L_3$, $8L_3$, $9L_3$, and $10L_3$ positions. This group has a difference in the relative knob frequencies between the collections of northern and southern Guatemala [Appendix Figures 31, 34, 37, and 39]. The large knobs, in general, showed predominance over the other knob types in the populations of southern regions. In the northern region, there were usually small knobs or the knobless condition in various frequency combinations in different positions with extremes as in the $4S_2$ position with a predominance of the small knobs, and $8L_3$ and $9L_3$ which showed a predominance of the knobless condition. The large and medium knobs were in low frequencies and, even in some cases [$5L_2$, $9L_3$, and $10L_3$ positions], they were absent. There are two variants of the general pattern shown by the $5L_2$ and $7L_3$ positions in populations from southern Guatemala. The former position showed a predominance of the knobless condition, but the large and the medium knobs were still found in relatively high frequencies. A similar situation was shown by the $7L_3$ position but in this case the small knobs also formed a considerable proportion of the knob polymorphism.

When the knobs located on the two arms of the same chromosome are compared within and between the populations of the two Guatemalan regions, relationships similar to those observed in chromosomes of Mexican teosinte are obtained. Two distinct situations are found in Guatemala teosinte:

1. The comparison of the $1S_3$ with $1L_3$ and $3S_2$ with $3L_3$ positions show that populations of both regions possess high knob frequencies on the short arm of the chromosomes but knobs on the long arm are absent in populations of southern Guatemala and almost absent in populations of northern Guatemala [Appendix Figures 32 and 33]. 2. When similar comparisons are made between the 7S with $7L_3$, 8S with $8L_3$, and 9S with $9L_3$ positions, it is observed that the southern populations have no knobs on the short arms but high knob frequencies are found in the long arms, while in the north the reverse occurs, that is, the short arms have many knobs and the long arms tend to have few knobs as in $8L_3$ and $9L_3$ positions, or high frequency of small knobs as in $7L_3$ position [Appendix Figures 36, 37, 38, and 39].

These observations seem to strengthen the idea already suggested when the Mexican teosinte was analyzed, that knobs have a kind of compensatory and/or complementary function that confers different adaptive values to the populations growing under different environmental conditions.

<u>Abnormal chromosome 10</u>. Two types of abnormal chromosome 10 are known in teosinte [Longley, 1937]. One of the types is common to both maize and teosinte and consists of a distal extra segment of chromatin in the long arm possessing a subterminal large knob. The second type which has been found only in Mexican teosinte populations differs from the first type in that the extra segment having the subterminal large knob also has a small or medium knob terminating it. In order to facilitate the distinction between these two types of abnormal chromosome 10, it is proposed to call the first as type I and the second as type II [Text Figure 5B].

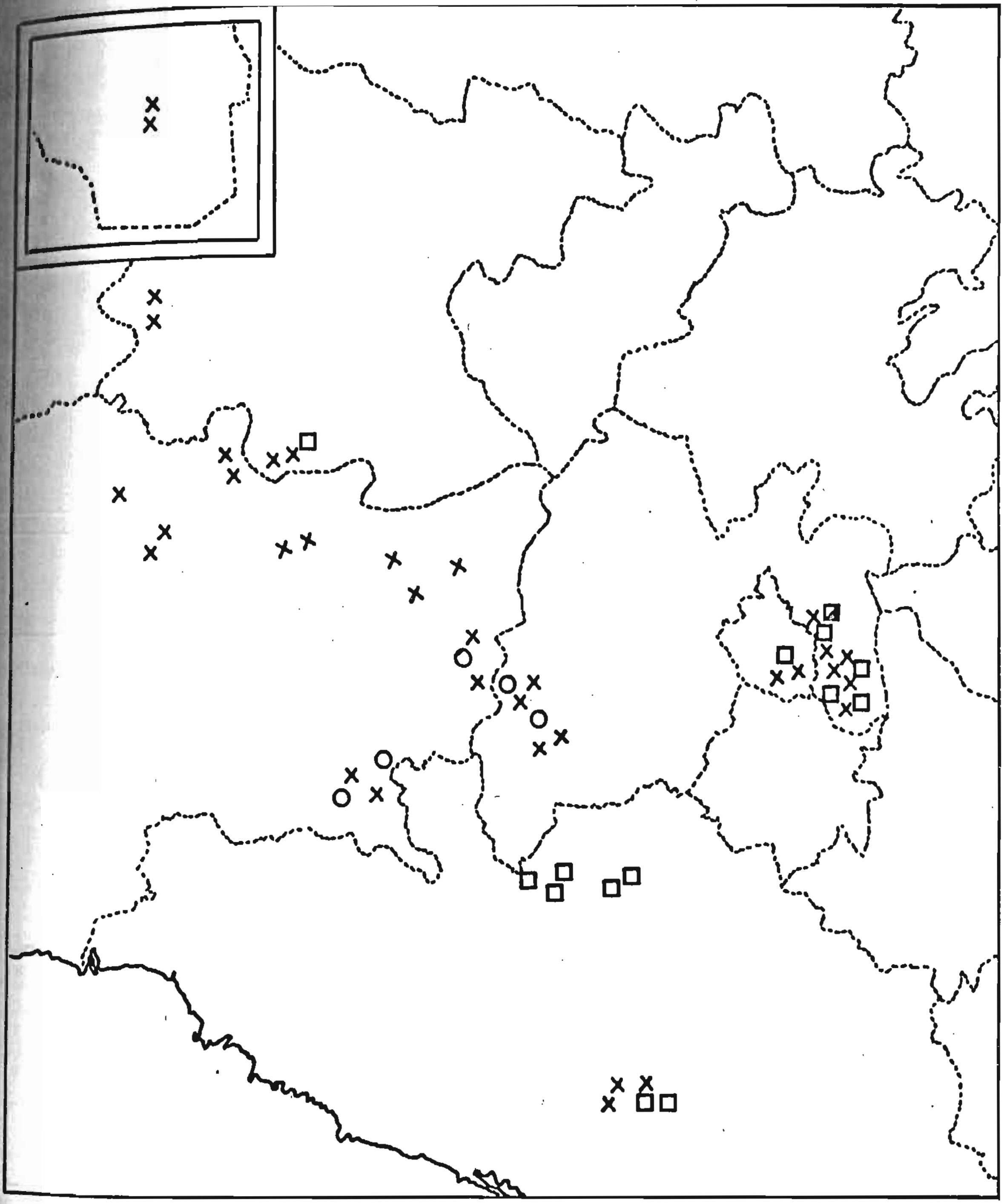

FIGURE 6. Geographical distribution of the type I [circles] and type II [squares] abnormal chromosomes 10 in collections of Mexican teosinte.

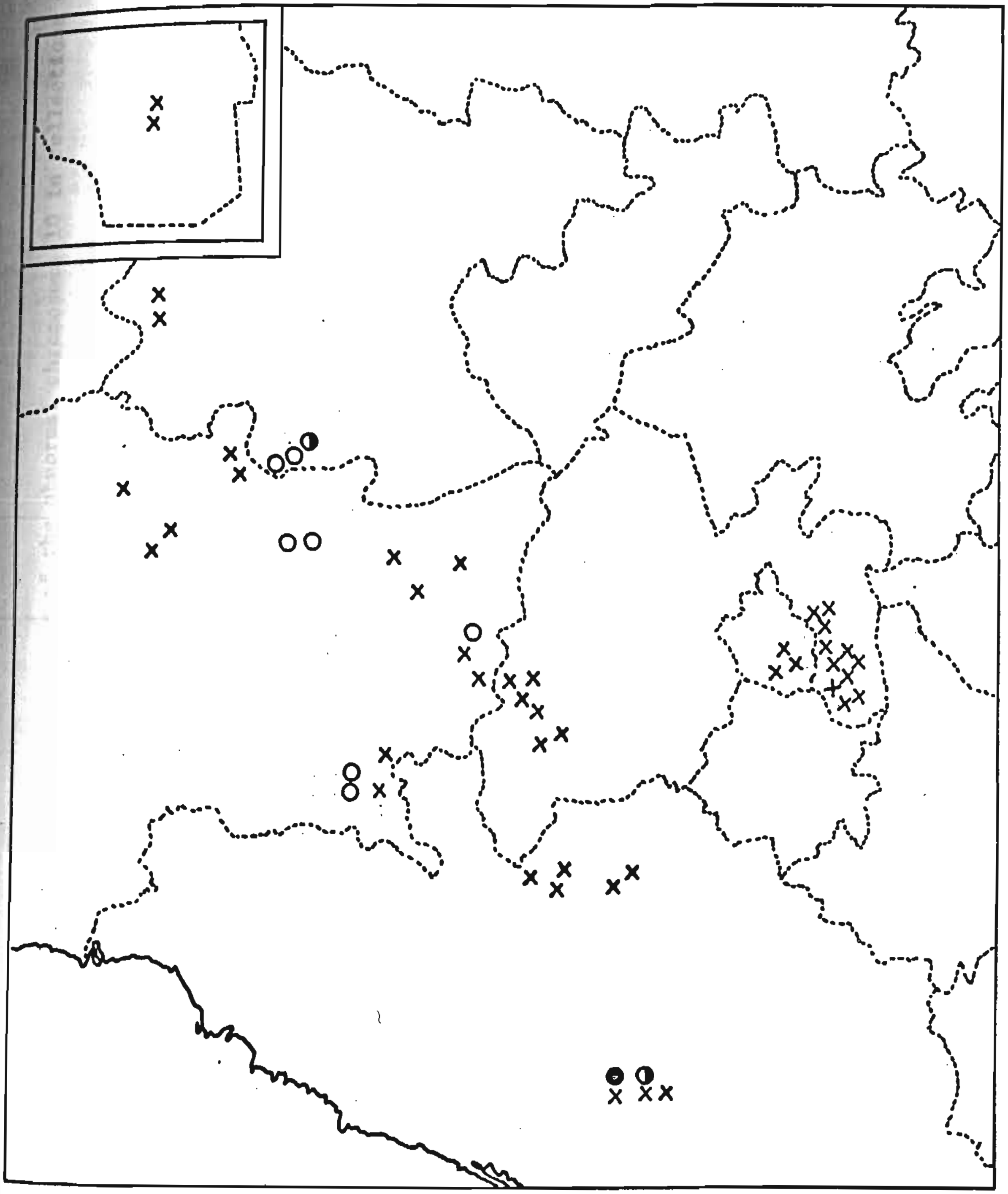

FIGURE 7. Geographical distribution of B chromosomes in collections of Mexican teosinte.

TABLE 7. Distribution of the two types of the abnormal chromosome 10 in collections of teosinte from different regions of Mexico.

REGIONS	NO. COLLECTIONS			NO. CHROMOSOMES		
	With	Without	Total	Type I	Type II	Total
Nobogame, Chihuahua	0	2	2	0	0	32
Western Guanajuato	0	2	2	0	0	20
S. Guanajuato-N. Michoacan	1	9	10	0	2	98
N. E. Michoacan	0	3	3	0	0	28
E. Michoacan-W. Mexico	3	6	9	4	0	98
Huetamo, Michoacan	2	2	4	2	0	50
Northern Guerrero	5	0	5	0	5	76
Central Guerrero	2	3	5	0	5	52
Chalco, Mexico	6	8	14	0	11	166
TOTALS	19	35	54	6	23	620

As shown in Text Table 7 and in Text Figure 6, the type I abnormal chromosome 10 has been found distributed only in populations from the eastern and the Huetamo regions in the state of Michoacan, and the western state of Mexico. On the other hand, the type II abnormal chromosome 10 was found in populations from the state of Guerrero and the Chalco region. Only one collection of the Guanajuato-N. Michoacan region showed the type II abnormal chromosome 10. In all cases, the two types of abnormal chromosome 10 were found in low frequencies in the collections possessing them.

It is of importance to emphasize the fact that both types of abnormal chromosome 10 were found in populations from separate regions and that in no one case both chromosome types were found coexisting in the same population or in different populations within the same general area. From this, it is clear that they are not distributed at random, indicating that some unknown set of factors maintain differentially segregated the two types of abnormal chromosome 10 into populations of different regions. This fact also suggests that the two types of abnormal chromosome 10 not only differ in their morphology, but also they may have different gene complexes.

B chromosomes. The regional distribution of the B chromosomes is given in Text Table 8, and the relative frequency distribution of each collection studied is shown in Text Figure 7. This type of supernumerary chromosomes were found from a particular sub-region of the Guanajuato-N. Michoacan region to the S.E. Michoacan region, and again in Mazatlan region of central Guerrero. The western portion of the Guanajuato-N. Michoacan, the western state of Mexico, the northern state of Guerrero, and the Chalco regions showed absence of B chromosomes. Therefore, although the B chromosomes do not follow any special distribution pattern in regions of Mexico, it is apparent that they are not distributed at random because populations of some regions tend to possess them and others do not.

The B chromosomes were not found in any of the collections of the Guatemalan teosinte examined.

In summary, the analysis of the knob frequency distribution in teosinte populations from Mexico and Guatemala have shown that knobs at different positions on the chromosomes are not distributed at random, but follow certain patterns. Some of these patterns are general for knobs of several positions, and others are more specific for a given position. The pattern differences also are found when the knob size is considered. For a particular knob position populations of some regions possess chiefly large knobs, while other regions have mostly small knobs or the knobless condition.

Another type of knob distribution pattern has been shown when two or more knob positions are considered together. In these cases, three situations occur: 1] knobs at one position prevail in a given region while those at the other position are absent, while the reverse is observed in other regions; 2] knobs at the two positions occur in populations of the same region; and 3] a combination of 1] and 2]. It seems that a compensatory and/or complementary effects are reflected in these types of knob distribution patterns.

Teosinte populations of any major region, as a whole, have a unique

TABLE 8. Distribution of B chromosomes in collections of teosinte from different regions of Mexico.

REGIONS	NO. COLLECTIONS			NO. PLANTS		
	With	Without	Total	With	Without	Total
Nobogame, Chihuahua	0	2	2	0	16	16
Western Guanajuato	0	2	2	0	10	10
S. Guanajuato-N. Michoacan	5	5	10	7	42	49
N. E. Michoacan	1	2	3	1	13	14
E. Michoacan-W. Mexico	1	8	9	1	48	49
Huetamo, Michoacan	2	2	4	4	21	25
Northern Guerrero	0	5	5	0	38	38
Central Guerrero	2	3	5	8	18	26
Chalco, Mexico	0	14	14	0	83	83
TOTALS	11	43	54	21	289	310

combination of knobs that most probably is the result of the action of natural selection in diverse ways, but specific for each region.

The results obtained with the knobs seem to be confirmed and substantiated by the distribution of the abnormal chromosome 10 and B chromosomes.

Knob Distribution in Maize

Geographical and racial distribution. The geographical distribution of the relative frequencies of the knobs at different positions on chromosomes of maize collections from central Mexico has shown that there exist several knob groups which show various distribution patterns. These patterns, however, in many cases are not sharply distinct from each other but showed variable degrees of intergradation.

In the first place, there is a large group of knobs at different positions [e.g., the large, medium and small knobs of the $1S_2$ and 9S positions; the large knobs of the $2L_1$, $3L_1$, $4L_1$, $5L_1$, $7L_1$, and $8L_1$ positions; and the small knobs of the $6L_2$ and $6L_3$ positions] that were found widely distributed in relatively high frequencies in maize populations of central Mexico. This general distribution of these knobs is interrupted by relatively low frequencies shown by them in a variable regional extension having a center about the Toluca Valley in the western part of the state of Mexico [Appendix Figures 19A, 22A, 25C, 26C, 28A, 29A, B, and C].

This type of distribution pattern is a reflection of the fact that populations of many races of maize, with the exception of Cacahuacintle, possess these knobs in a comparatively high frequency in most of the regions of central Mexico [Text Tables 9 and 10].

Contrary to the distribution pattern shown by the knobs given above, the knobless condition at the same positions, and also at many other positions, are predominant in maize populations of the region with a center in the Toluca Valley showing, in general, a relatively lower frequency elsewhere [Appendix Figures 17D through 29D]. This is again a consequence of the fact that in the highlands of the Central Mesa of Mexico there are races like Cacahuacintle, Cónico, and Chalqueño that, in general, possess higher frequencies of the knobless positions than in the other races [Text Tables 9 and 10].

Another group of knobs [the medium knobs of the $2L_1$, $3L_1$, $4L_1$, $5L_1$, $7L_1$, and $8L_1$, and the large, medium and small knobs of the $9L_2$ positions] have been found in relatively higher frequencies in maize populations of Guerrero, but especially those of its coastal regions, and also in populations of the regions of northern state of Hidalgo, southeastern state of San Luis Potosí, and the northwestern state of Veracruz. This region is commonly called La Huasteca. Nevertheless, several populations from other regions, especially the Bajío region of Guanajuato, northern state of Michoacan, and western state of Querétaro have also shown a relatively high frequency of some of these knobs [Appendix Figures 19B, 22B, 28B, and 29A, B, and C]. The fact that the knobs concerned here have been found in relatively higher frequencies in populations of the related races Tuxpeño in La Huasteca region, and of Vandeño in Guerrero, explains why these knobs are frequent in these regions. The Tuxpeño race predominates in the eastern coast of Mexico and Vendeño is one of the major maize types in central and coastal Guerrero. Also these knobs seem to have been introduced into populations of the races like Celaya, Cónico Norteño, and

TABLE 9. Average percent frequencies of different size knobs at the $2L_1$, $3L_1$, $4L_1$ positions as found in several races of maize from central Mexico.

RACE	NO. COL.	KNOB POSITION AND SIZE												TOTAL NO. CHROM.
		$2L_1$				$3L_1$				$4L_1$				
		l	m	s	o	l	m	s	o	l	m	s	o	
Cacahuacintle	3	1.6	1.6		96.7	8.3	1.6	3.3	86.7	13.3	8.3	3.3	75.0	60
Celaya	7	47.8	16.3	1.1	34.8	39.1	30.4	2.2	28.2	76.1	11.9		11.9	92
Chalqueño	7	18.0	8.3	2.8	70.8	44.4	6.9	1.4	47.2	62.5	11.1		26.4	72
Cónico	9	14.5	11.3	0.8	73.4	35.5	12.1	5.6	46.8	37.1	18.5	8.0	36.3	124
Cónico Norteño	12	47.4	10.5	1.7	40.3	53.5	11.4		35.1	73.7	10.5	0.9	14.9	114
Maíz Ancho	8	43.4	5.2		51.3	52.6	2.6		44.7	77.6	5.2		17.1	76
Pepitilla	26	35.8	9.9	1.4	52.8	41.6	8.4	0.5	49.5	77.3	8.5	0.5	13.7	214
Tuxpeño	8	47.5	30.0	2.5	20.0	24.4	25.6	6.1	43.9	39.7	41.0	3.8	15.4	82
Vandeño	14	39.9	24.5	2.6	32.9	19.7	27.2	1.3	51.7	65.3	18.0	1.3	15.3	228

TABLE 10. Average percent frequencies of different size knobs at the $5L_1$, $7L_1$, $8L_1$ positions as found in several races of maize from central Mexico.

RACE	NO. COL.	KNOB POSITION AND SIZE												TOTAL NO. CHROM.
		$5L_1$				$7L_1$				$8L_1$				
		l	m	s	o	l	m	s	o	l	m	s	o	
Cacahuacintle	3	18.3	11.7	28.3	41.6	11.7		1.6	86.7	5.0	5.0	3.3	86.7	60
Celaya	7	61.9	21.7	2.2	14.1	60.9	20.6	6.5	11.9	48.9	30.4		20.6	92
Chalqueño	7	61.1	9.7	4.1	25.0	68.0	8.3	1.4	22.2	19.4	30.5	1.4	48.6	72
Cónico	9	39.5	22.6	14.5	23.4	28.2	19.3	11.3	41.1	16.1	16.1	4.0	63.7	124
Cónico Norteño	12	76.3	8.8	1.7	13.1	64.0	16.6	0.9	18.4	50.9	23.7		25.4	114
Maíz Ancho	8	85.5	5.2		9.2	84.2	2.6		13.1	51.3	10.5	1.3	36.8	76
Pepitilla	26	81.1	1.4	6.1	11.3	64.9	7.9	2.8	24.3	41.5	16.0	3.3	39.1	214
Tuxpeño	8	40.0	47.5	3.7	8.7	39.0	46.3		14.6	34.1	37.8	3.6	24.4	82
Vandeño	14	62.3	22.3	3.1	12.3	39.5	31.6	4.8	24.1	12.3	32.0	4.8	50.9	228

Cónico growing in the Bajío region and the Central Mesa. They possessed these knobs in higher frequencies than populations of other races of the same region, such as Chalqueño and Pepitilla, but lower frequencies than the Tuxpeños and the Vandeños [Text Tables 9 and 10].

The large, medium and the small knobs of the $1L_1$, $2S_1$, $3S_1$, and $6L_1$ positions, and the small knobs of the $10L_2$ positions, form a group of knobs that were found mostly in maize populations of different races from the highlands of Central Mesa and the Bajío regions [Maps A, B, and C of Appendix Figures 17, 18, 20, and 24]. These knobs have usually been found in low frequencies and in scattered populations throughout these two regions. However, two of these knobs, the large knob at the $2S_1$ position and the medium knob at the $6L_1$ position, but especially the former one, appeared in higher frequencies in many populations. Also the large knobs at the $2S_1$ position were found with considerable frequency in populations of Pepitilla and Maíz Ancho, mostly in the state of Morelos. The Chalco region, which is connected to the northeastern part of the state of Morelos, had populations showing a high frequency of the large knobs at $2S_1$ position suggesting a probable germplasm flow from the highland races such as Chalqueño into the Pepitilla and Maíz Ancho [Appendix Figure 18A].

The large and the medium knobs at the $6L_3$ position have been found distributed in maize populations mainly from two regions, namely the northeastern section of the Balsas Basin and the Bajío region. The Central Mesa and the coastal regions of Guerrero showed some populations having these knobs, but it seems in lower frequencies than in the Balsas and the Bajío regions [Appendix Figure 26A and B]. One important fact shown by these knobs, particularly the large knobs, is that they have been found mostly

TABLE 11. Average percent frequencies of different size knobs at the $6L_1$, $6L_2$, and $6L_3$ positions as found in several races of maize from central Mexico.

R A C E	NO. COL.	KNOB POSITION AND SIZE												TOTAL NO. CHROM.
		$6L_1$				$6L_2$				$6L_3$				
		l	m	s	o	l	m	s	o	l	m	s	o	
Cacahuacintle	3		6.6	1.6	91.7				100.0		1.6	1.6	96.7	60
Celaya	7	2.2	4.3	8.7	84.8			33.7	66.3	2.2	13.0	36.9	47.8	92
Chalqueño	7	2.8	13.9	6.9	76.4			6.9	93.0		4.1	20.8	75.0	72
Cónico	9	2.4	9.7	1.6	86.3			7.2	92.7		6.4	18.5	75.0	124
Cónico Norteño	12	4.4	17.5	4.4	73.7			28.9	71.0	4.4	15.8	22.8	57.0	114
Maíz Ancho	8		2.6		97.4		1.3	17.1	81.6	7.9	19.7	11.8	60.5	76
Pepitilla	26		6.6		93.4			22.6	77.3	8.0	14.6	19.3	58.0	212
Tuxpeño	8			1.2	98.8			50.0	50.0		9.7	47.5	42.7	82
Vandeño	14		0.4	1.3	98.2		1.7	37.7	60.5	0.4	13.1	31.6	54.8	228

in the races Pepitilla and Maíz Ancho. Most of the collections of Pepitilla and all of the Maíz Ancho studied were from the Balsas region. In the Bajío, most of these knobs of the $6L_3$ position were found in populations of the races Cónico Norteño and Celaya. Nevertheless, all of the 5 collections of Pepitilla from the Bajío studied showed either the large or the medium knob at this position [Text Table 11].

Another important fact shown by the data in Text Table 11 is that the general distribution trends of the knobs of the $6L_3$ position, and those of the $6L_1$ position, follow alternative patterns. The large and medium knobs of the former position tend to be concentrated in the maize populations of races from regions of intermediate altitudes, such as Pepitilla, Maíz Ancho, Cónico Norteño, and Celaya, and also in races of the lowlands, such as Tuxpeño and Vandeño. On the other hand, the large and medium knobs of the $6L_1$ position tend to be more prevalent in races of the highlands, like Chalqueño, Cónico, and Cacahuacintle, and also in races from regions of intermediate altitudes of the Bajío, such as Celaya and Cónico Norteño. These distribution patterns seem to suggest that in the Bajío region there are factors that favor the coexistence of knobs at both positions, but in the Central Mesa there are no factors favoring the presence of the knobs of the $6L_3$ position and, on the other hand, in the Balsas Basin region those knobs of the $6L_1$ position do not find favorable conditions for becoming established. The knobs of the $1L_1$, $2S_1$, $3S_1$, and the $10L_2$ position have similar relationships to the large and medium knobs of the $6L_3$ position because they have similar distributional patterns as those of the $6L_1$ position as described above. However, as mentioned before, the large knobs at the $2S_1$ position have become established in

TABLE 12. Frequencies of the abnormal chromosome 10 and of B chromosomes in collections of several races of maize from regions of central Mexico.

RACE	No. Col.	Chromosome 10			B Chromosomes				
		Normal %	Abnormal %	Total No. Chrom.	Plants		Average B's Plant	Total No. Plants	No. Col. w/B's
					With %	Without %			
Cacahuacintle	3	100.0		60	6.6	93.3	0.13	30	1
Celaya	7	96.7	3.2	92	17.4	82.6	0.35	46	3
Chalqueño	7	90.3	9.7	72	2.8	97.2	0.05	36	1
Cónico	9	99.2	0.8	124	16.1	83.9	0.27	62	4
Cónico Norteño	12	97.4	2.6	114	33.3	66.6	0.77	57	7
Maíz Ancho	8	100.0		76	21.0	78.9	0.39	38	4
Pepitilla	26	98.6	1.4	214	23.3	76.6	0.44	107	13
Tuxpeño	8	96.3	3.6	82	7.3	92.7	0.24	41	2
Vandeño	14	99.1	0.9	228	8.8	91.2	0.13	114	6

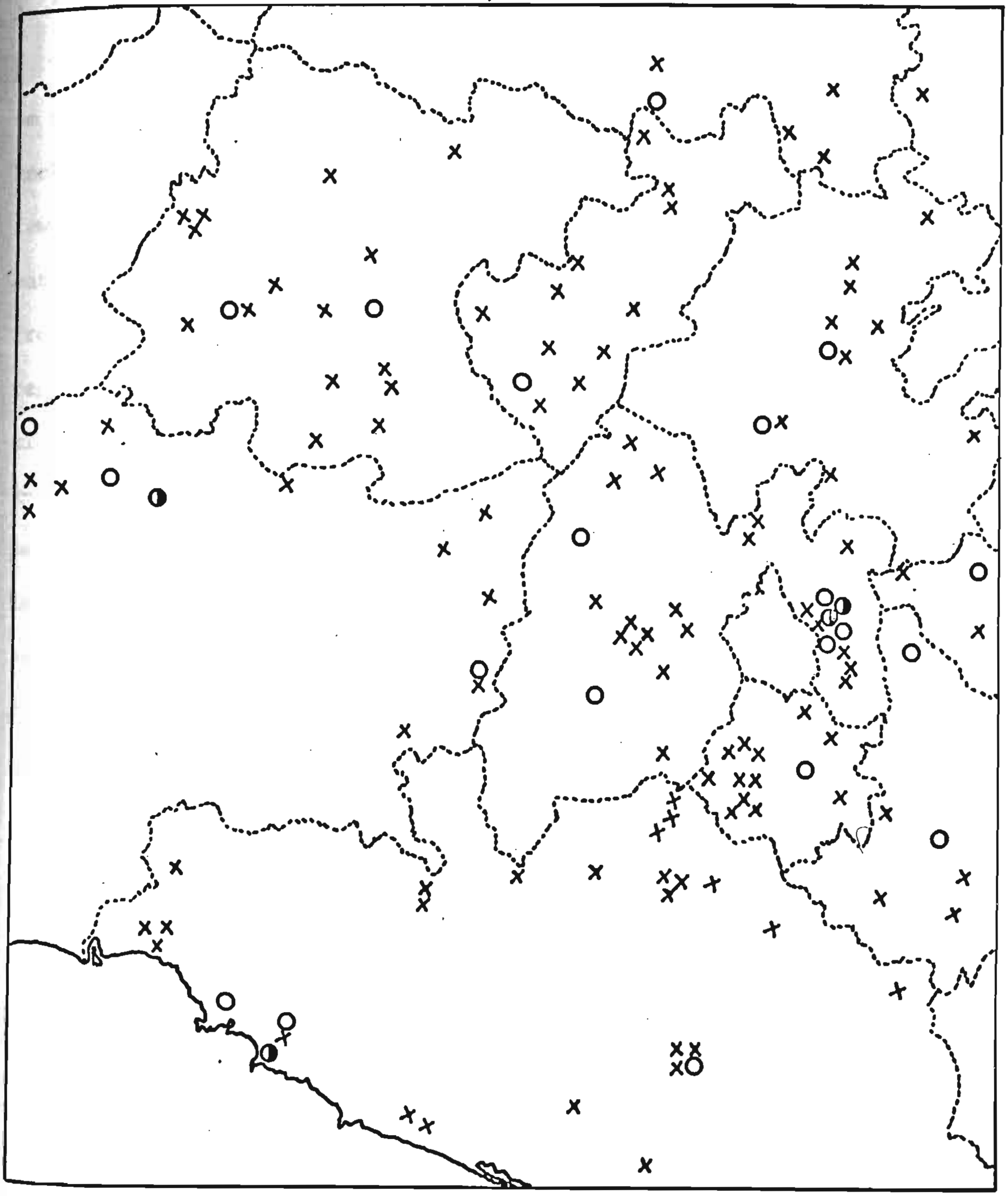

FIGURE 8. Geographical distribution of the abnormal chromosome 10 in collections of maize from central Mexico.

relatively high frequencies in populations of the races Pepitilla and Maíz Ancho of the Balsas Basin region.

In addition, there is another group of knobs [e.g., the large, medium and small knobs at the $4S_2$, $5S_1$, and the 7S positions, and the medium knob at the $6L_2$ position] which occur generally in low frequencies in a few of the collections of maize from central Mexico included in the present study. Most of the collections having these knobs, however, have been from localities of the Balsas Basin region and/or from central and coastal regions of the state of Guerrero. Relatively speaking, only a few collections from the Central Mesa and the Bajío regions possessed some of these knobs [Appendix Figures 21, 23, 25, and 27]. This kind of distribution pattern suggests that these knobs represent a migration from maize populations that are growing in more southern regions. In the next chapter, evidence will be given showing that this northward migration of germplasm from the races Zapalote Chico and Zapalote Grande of the Oaxaca-Chiapas region of southern Mexico is the best explanation for the presence of these knobs in regions of central Mexico.

Abnormal chromosome 10. Only the type I abnormal chromosome 10 was found in the maize populations analyzed in the present study. This chromosome type is distributed very sparcely in populations scattered all over the regions of central Mexico considered here without showing any apparent distribution pattern [Text Figure 8 and Text Table 12].

B chromosomes. This type of unusual chromosome has been found to be present in higher frequencies than that shown by the abnormal chromosome 10. Furthermore, contrary to the abnormal chromosome 10, it seems that

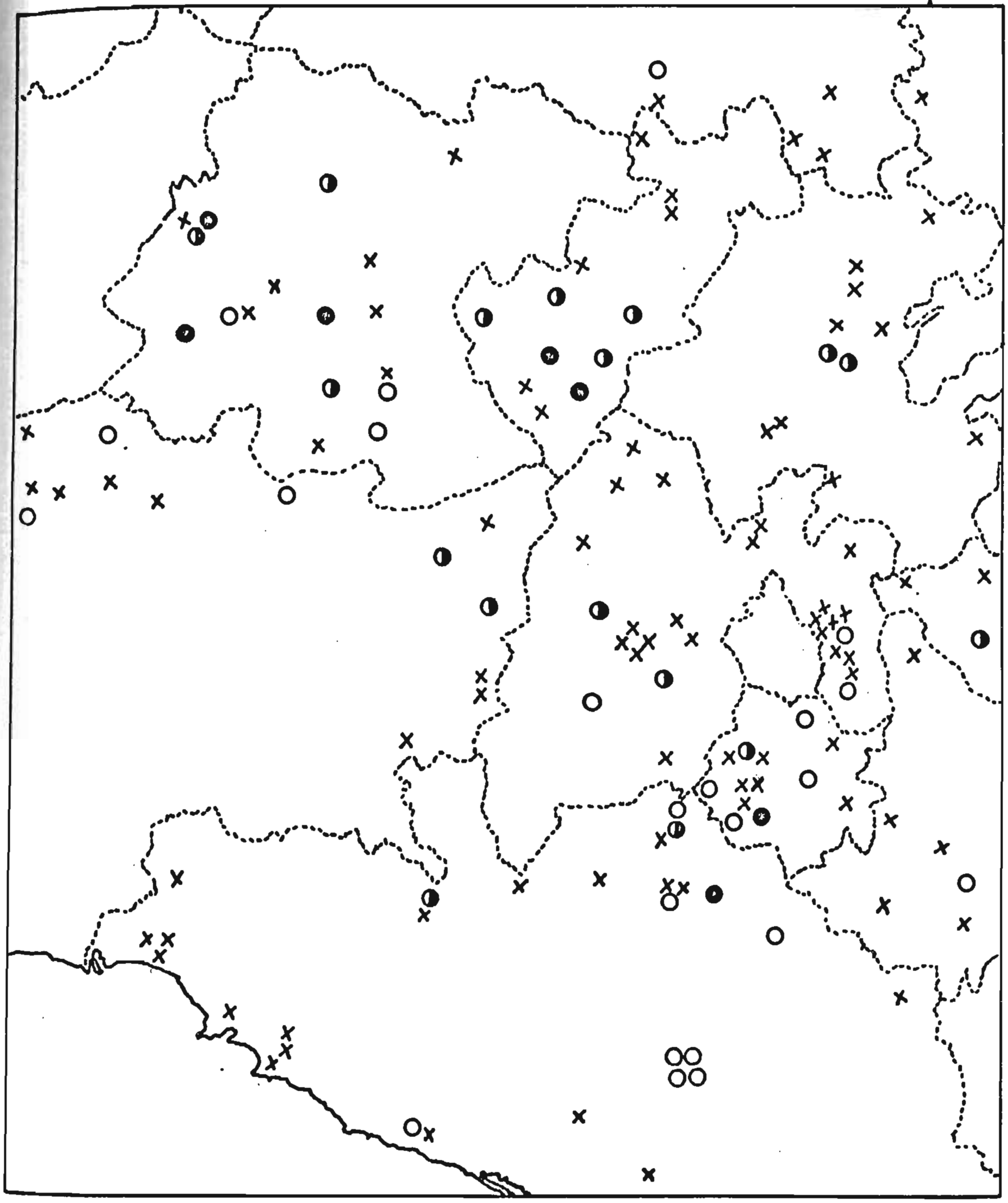

FIGURE 9. Geographical distribution of B chromosomes in collections of maize from central Mexico.

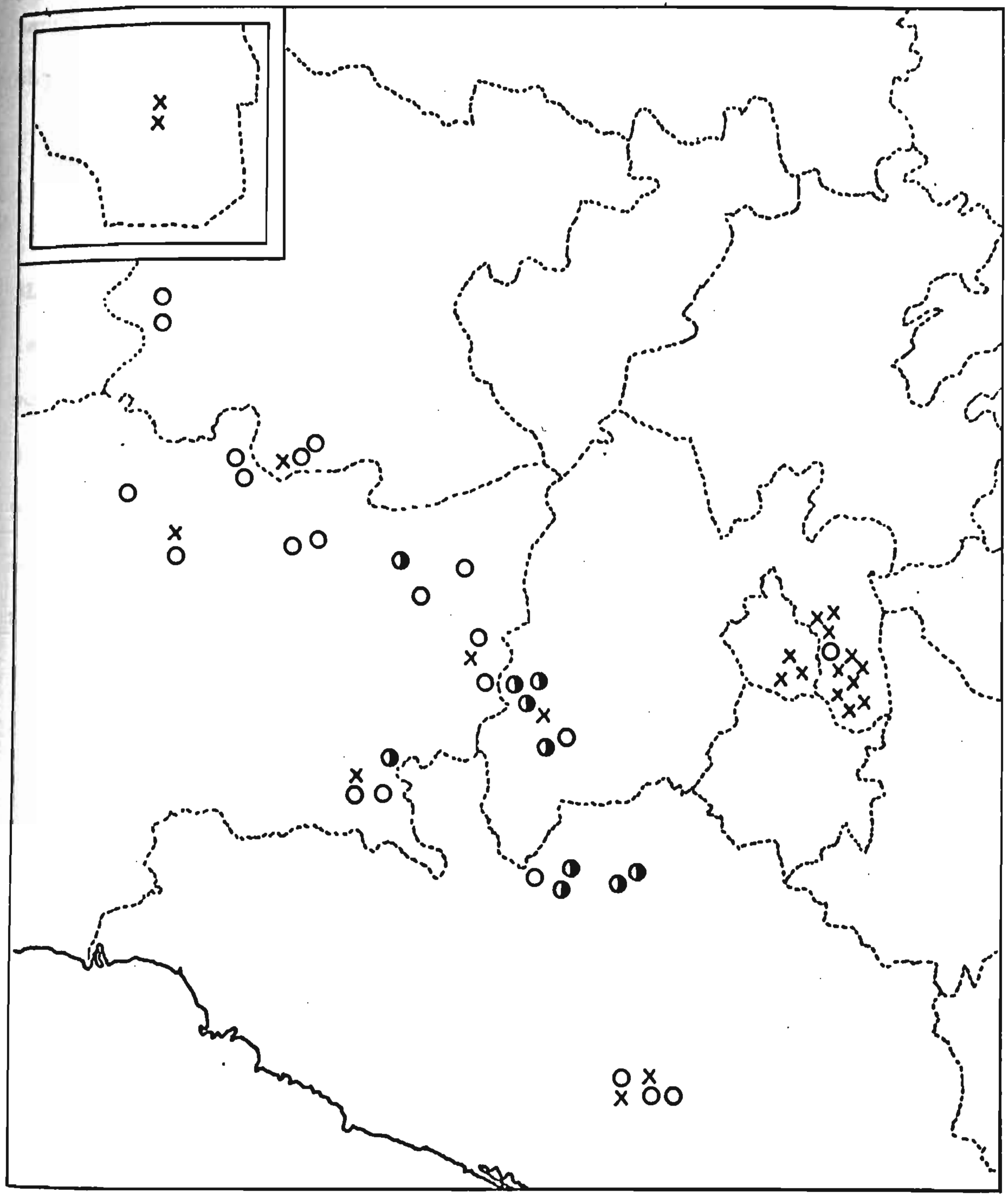

FIGURE 10. Geographical distribution of the small knobs at the $1L_2$ position in collections of teosinte from Mexico.

the B chromosomes do show a definite distribution pattern. This pattern happens to be similar to that shown by the large and medium knobs of the $6L_3$ positions [Text Table 12 and Text Figure 9].

Comparative Knob Distribution in Maize and Teosinte

It has been shown that there are several positions [e.g., $1S_2$, $2L_1$, $3L_1$, $4L_1$, $5L_1$, $7L_1$, $8L_1$, and 9S] that possessed knobs, especially of the large size, in a wide range of populations of both maize and teosinte from most of the regions of central Mexico. In many of these regions in Guanajuato, Michoacan, Mexico and Guerrero, populations of both species are usually growing in close sympatry. This close relationship between the knobs at these positions in both species could indicate that these knobs may have similar adaptive values under different genetic and environmental conditions.

Other knobs at different positions, however, have shown that they are present in different frequencies in populations of either maize or teosinte growing in different regions of central Mexico.

This kind of relationship can be illustrated by making comparative analysis of the knob distributions at several positions as found in populations of both maize and teosinte.

The $1L_2$ position is one that showed only small knobs in teosinte populations of most of the regions. These knobs were found in relatively high frequencies, especially in the regions of western state of Mexico and northern state of Guerrero [Text Figure 10]. In maize populations, the $1L_2$ position turned out to be knobless. This shows that the chromosomal segment having this knob does not introgress from teosinte to maize.

The $2S_1$ position is one which knobs were found showing different distribution patterns in populations of maize and teosinte in regions of central Mexico. Maize populations possessed knobs, especially the large ones, in high frequencies in the Central Mesa and the Bajío regions, and very low frequencies in the regions of Guerrero and southern state of Puebla [Appendix Figure 18]. The populations of the races Zapalote Chico and Zapalote Grande of the Oaxaca-Chiapas regions in southern Mexico, however, have been found to possess these knobs in high frequencies [Text Table 13]. On the other hand, teosinte populations showed high frequencies of knobs at this position in all the regions of the main range of teosinte distribution in central Mexico from Guanajuato through Guerrero, and also in the Chalco region.

This situation clearly indicates that the knobs at the $2S_1$ position found in low frequencies in maize populations in the state of Guerrero and in southern state of Puebla most probably represent migration of these knobs from two main sources. One source is in the maize populations of the Bajío and the Central Mesa. One of the probable migration routes followed by these knobs seems to be from the maize type of the race Chalqueño in the Chalco region through the races like Pepitilla and Maíz Ancho in the state of Morelos as indicated in the previous chapter [see also Appendix Figure 18]. The second source is in the Zapalotes of southern Mexico. There is, however, a possible third choice, that is, from teosinte populations of the state of Guerrero by the process of introgressive hybridization.

A similar situation as that of $2S_1$ position was found in the knobs at the $3S_1$ position. The knob frequencies in maize populations were low

TABLE 13. Knob frequencies for the $1L_1$, $2S_1$, $3S_1$, and $4S_2$ positions on chromosomes of maize and teosinte populations from two Mexican regions, Chalco in southeastern state of Mexico and Mazatlan in central state of Guerrero where both plant species grow in close sympatry. Also knob frequencies of maize populations of the races Zapalote Chico and Zapalote Grande from regions of the states of Oaxaca and Chiapas in southern Mexico are included for comparative purposes.

SPECIES AND REGION	No. Col.	KNOB POSITION AND SIZE								TOTAL NO. CHROM.
		$1L_1$				$2S_1$				
		l	m	s	o	l	m	s	o	
MAIZE										
Chalco, Mex.	10	4	5	3	114	48	7	0	71	126
Mazatlán, Gro.	4	0	0	0	124	10	2	4	108	124
Oaxaca-Chiapas	13*	0	5	8	135	81	15	0	52	148
TEOSINTE										
Chalco, Mex.	14	131	8	2	25	97	20	3	46	166
Mazatlán, Gro.	5	9	5	1	37	32	5	0	15	52

TABLE 13. [Continued]

SPECIES AND REGION	No. Col.	KNOB POSITION AND SIZE								TOTAL NO. CHROM.
		$3L_1$				$4S_2$				
		l	m	s	o	l	m	s	o	
MAIZE										
Chalco, Mex.	10	3	8	0	115	0	0	0	126	126
Mazatlán, Gro.	4	0	0	0	124	0	1	0	123	124
Oaxaca-Chiapas	13*	18	22	7	101	4	29	16	99	148
TEOSINTE										
Chalco, Mex.	14	1	21	0	144	31	9	2	124	166
Mazatlán, Gro.	5	18	1	0	33	12	9	2	29	52

*From unpublished data of McClintock, Blumenschein and Kato.

at this position and most populations possessing them are concentrated in the Bajío and the Central Mesa, while in the Guerrero-Morelos-Puebla regions comparatively few populations possess them [Appendix Figure 20]. Text Table 13 shows that the knobs at the $3S_1$ position have been found in relatively high frequencies in the races Zapalote Chico and Zapalote Grande in the Oaxaco-Chiapas region of southern Mexico. Contrasting with this situation in maize, the knobs at the $3S_1$ position in teosinte were found mainly in populations of the southeastern state of Michoacan, western state of Mexico and in the state of Guerrero. Only a few teosinte populations from Guanajuato and northern Michoacan had these knobs and in rather low frequencies. The teosinte populations of the Chalco region possessed mostly medium size knobs in moderate frequencies. The knob distributions at the $3S_1$ position, as described, seem to indicate quite clearly not only that these knobs have different adaptive values in different populations of either teosinte or maize, but also that the knobs found in teosinte populations most probably are not introgressing into populations of maize. Otherwise it has to be accepted that introgression is more intense in the Bajío and Central Mesa and less intense in Guerrero. However, the introgression process occurring in this way would have difficulties in explaining why these knobs are more frequent in maize than in teosinte in the highlands, and how the Zapalotes of Oaxaca-Chiapas region could have gotten these knobs since no teosinte population is known to occur in this region. Text Table 12 also shows that the maize and teosinte from Chalco region possessed knobs at the $3S_1$ position suggesting that they might represent introgression from teosinte to maize. However, in the Mazatlán region, these knobs were absent from maize but present in teosinte. It seems, therefore, that the knobs present in Chalco maize are not the result of introgression, even though it is not possible to discard the idea of introgression since it is known that in the Chalco region hybridization occurs at a higher rate than in Mazatlán.

The knobs at other positions seem to indicate more clearly that the knobs of both teosinte and maize have different adaptive values within and between species, and that introgression of these knobs does not occur between populations of these species. The knobs at the $4S_2$, $5S_1$, and 7S positions have been found in relatively high frequencies in different teosinte populations, as already described above. In the maize populations of central Mexico, however, these knobs appeared to be almost absent, with only a few exceptions [Appendix Figures 5, 7, 12, 21, 23, and 27]. These knobs, however, have been found in higher frequencies in populations of the races Zapalote Chico and Zapalote Grande in southern Mexico [Text Table 13]. The few knobs found in maize populations might represent introgression from teosinte. However, when populations of teosinte and maize from more restricted regions where it is known that they are and have been growing in close sympatry, probably for thousands of years, such as in Chalco region in southeastern state of Mexico and in Mazatlán region in central state of Guerrero, it becomes clear that such introgression does not occur. As shown in Text Tables 13 and 14, these knobs are present in teosinte but absent or almost so in maize populations of the Chalco and Mazatlán regions. The single medium knob at the $4S_2$ position, and large one at the 7S position found in maize from Mazatlán seem to have had their origin from the Zapalotes of Oaxaca rather than from

TABLE 14. Knob frequencies for the $5S_1$, $6L_2$, $6L_3$, and 7S positions on chromosomes of maize and teosinte populations from two Mexican regions, Chalco in southeastern state of Mexico and Mazatlan in central state of Guerrero where both plant species grow in close sympatry. Also knob frequencies of maize populations of the races Zapalote Chico and Zapalote Grande from regions of the states of Oaxaca and Chiapas in southern Mexico are included for comparative purposes.

SPECIES AND REGION	NO. COL.	KNOB POSITION AND SIZE								TOTAL NO. CHROM.
		$5S_1$				$6L_2$				
		l	m	s	o	l	m	s	o	
MAIZE										
Chalco, Mex.	10	0	0	0	126	0	0	4	122	126
Mazatlán, Gro.	4	0	0	0	124	0	2	28	94	124
Oaxaca-Chiapas	13*	17	13	0	118	4	49	70	25	148
TEOSINTE										
Chalco, Mex.	14	61	20	1	84	0	0	31	135	166
Mazatlán, Gro.	5	7	7	0	45	0	0	21	31	52

TABLE 14. [Continued]

SPECIES AND REGION	NO. COL.	KNOB POSITION AND SIZE								TOTAL NO. CHROM.
		$6L_3$				7S				
		l	m	s	o	l	m	s	o	
MAIZE										
Chalco, Mex.	10	0	1	15	110	0	0	0	126	126
Mazatlán, Gro.	4	1	28	23	72	1	0	0	123	124
Oaxaca-Chiapas	13*	0	21	91	36	69	24	7	48	148
TEOSINTE										
Chalco, Mex.	14	0	0	20	146	42	27	6	91	166
Mazatlán, Gro.	5	40	4	0	8	0	2	1	49	52

*From unpublished data of McClintock, Blumenschein and Kato.

teosinte. There are two main reasons for this interpretation: 1] there is no indication of introgression of these knobs in the Chalco region where it is known that hybridization occurs at higher frequency than in Guerrero; and 2] the large knobs at the 7S position were absent in teosinte from the Mazatlán region.

The medium size knobs at the $6L_2$ position in both maize and teosinte have been found in low frequencies as described above and shown in Appendix Figures 10 and 25. Nevertheless, when teosinte and maize populations of Chalco and Mazatlán are compared with regard to these knobs, it is observed that they are present only in maize of Mazatlán in low frequency but absent from the teosinte of both regions. They have been found, however, in high frequencies in maize populations of the races Zapalote Chico and Zapalote Grande [Text Table 14].

A similar situation is found when the knobs at the $6L_3$ position are compared in the same way as those of the $6L_2$ position. In the Chalco region, teosinte showed only small knobs while maize possessed mostly small knobs and one medium size knob. In Mazatlán, the teosinte has shown high frequency of large knobs with the medium knobs in low frequency. The small knobs were absent. Contrary to this, the maize populations had medium and small knobs in relatively high frequencies, while only one large knob was found out of 128 chromosomes observed. The Zapalotes of Oaxaca-Chiapas region possessed medium and small knobs in high frequencies but no large knobs were found [Text Table 14].

These data of chromosome 6, therefore, seem to indicate that there is no introgression between populations of teosinte and maize in the Chalco and Mazatlán regions. The single large knob found in maize from Mazatlán could have had its origin in some populations of the race Pepitilla or Maíz Ancho in the Balsas Basin. However, the possibility for it to have had introgressed from teosinte cannot be ruled out with the present data.

It is well known, as well as confirmed in the present studies, that the Guatemalan teosintes have knobs only at terminal positions of both the long and the short arms of their chromosomes. With the exception of some of the knobs [e.g., at the $4S_2$, 7S, and 9S positions] all others, which total 14 positions are not known to show knobs in maize populations from Guatemala or from any other maize populations so far examined [Longley and Kato, 1965; McClintock, 1959, 1960; Kato and Blumenschein, 1967; McClintock, Blumenschein and Kato, unpublished; and others]. It seems clear, therefore, that no common introgression, of at least 14 or so chromosomal segments, between maize and teosinte occurs in Guatemala.

In summary, the comparative analysis of knob distributions in populations of maize and teosinte strongly indicate that, in most of the cases, there are good evidences supporting the conclusion that the knobs and probably the chromosomal segments adjacent to them are not introgressing between populations of these two plant species. There were several cases, however, where the possibility for introgression to have occurred cannot be ruled out. This is because the present data show only indirectly the possibility of whether or not knob introgression between maize and teosinte populations occurs.

Chromosome Inversions

Teosinte populations. During the cytological determination of knob constitutions of the teosinte collections, no special hybrids were made to find out whether these collections possessed inversions or other kinds of chromosomal aberrations. Nevertheless, in two cases, heterozygous inversion loops were observed. The first one was the inversion on the short arm of chromosome 9 [In9S] in a collection from Zoquiapan in the Chalco region [Plate IV, Figure 33, and Text Table 16]. The second instance was an inversion on the short arm of chromosome 8 [In8S] in a collection from Manuel Doblado in the state of Guanajuato.

These two observations are important, not only because they confirm the findings about the presence of these inversions by other investigators [Ting, 1964; Wilkes, 1967], but also because they show without any doubt that in teosinte populations of Chalco and Guanajuato, both the inverted and the non-inverted segments of the corresponding chromosomes can occur together. Ting [1964] reported that these inversions were found in a homozygous condition in the teosinte plants from Chalco region and from Durango in Mexico. The present observations, however, also indicate that more extensive studies should be done before any conclusions can be drawn regarding the frequencies in which these inversions are present in different populations.

In the experimental maize x teosinte hybrids used in these studies, some of the inversions found by other investigators were confirmed and also some new inversions were found. Among the former ones are the In1Lb, In8S, and In9S. The In1Lb was found in teosinte plants from Jutiapa in southern Guatemala confirming the previous report by Ting [1965]. This inversion, however, was also found in these studies in teosinte plants from Tzisbaj in the department of Huehuetenango in northern Guatemala

TABLE 15. Length of the inversions InlLa of Nobogame teosinte and InlLb of N. Guatemala teosinte as measured in maize x teosinte F_1 hybrids.

Cell No.	LENGTH				
	Long Arm	Proximal [microns]	Inverted	Distal	Inv./L.Arm %
Nobogame					
1	60.9	27.6	12.6	20.7	20.7
2	47.0	18.0	13.0	16.0	27.6
3	46.5	20.2	11.5	14.8	24.7
$\bar{x}$	51.5	21.9	12.4	17.2	24.3
N. Guatemala					
1	65.0	29.5	11.4	23.7	17.5
2	56.1	22.0	9.6	24.5	17.1
$\bar{x}$	60.5	25.7	10.5	24.1	17.3

TABLE 16. Length of the In9S inversion in Nobogame and S. Guatemala teosintes as measured in maize x teosinte F_1 hybrids. The measurement for Chalco is from a teosinte plant with the heterozygous inversion.

Cell No.	LENGTH Short arm	Proximal [microns]	Inverted	Inv./S.arm %
Nobogame				
1	19.0	4.0	15.0	78.9
2	19.8	6.5	13.3	67.2
$\bar{x}$	19.4	5.2	14.1	73.0
Chalco				
1	16.6	4.0	12.6	75.9
S. Guatemala				
1	13.7	5.0	8.7	63.5

TABLE 17. Length of the In8S inversion in Nobogame teosinte as measured in maize x teosinte F_1 hybrids.

Cell No.	LENGTH Short arm	Proximal [microns]	Inverted	Inv./S.arm %
17K-1	15.0	2.5	12.5	83.3
2	16.4	4.5	11.9	72.5
3	15.5	2.7	12.8	82.6
4	14.4	2.3	12.1	84.0
5	14.4	3.6	10.8	75.0
6	14.6	2.7	11.9	81.5
$\bar{x}$	15.0	3.0	12.0	79.8
25K-1	17.6	3.2	14.4	81.8
2	15.9	5.6	10.3	64.8
3	14.4	1.8	12.6	87.5
$\bar{x}$	15.9	3.5	12.4	78.0

[Plate IV, Figures 36, 37, and 38]. Some preliminary measurements [Text Table 15] showed that the inverted segment was approximately 10.5 μ in length, or 17.3% of the length of the long arm. Ting [1965] reported 18.1 μ as the average length of the inverted segment, or 22% of the length of the long arm. This difference might not be real but probably is due to sampling error since both Ting's and the present number of measurements are few and the variability in length of pachytene chromosomes is high, as shown in a previous chapter. These findings clearly show that both northern and southern Guatemala teosinte populations should have had a common ancestral population. This is so if the In1Lb actually refers to the same inversion in populations of both Guatemalan regions and because it is generally accepted that the probability of forming the same inversion by independent events is negligible.

The In8S was found in populations of Nobogame teosinte confirming the findings of Ting [1958a, 1964]. The measurements made in the present study, as given in Text Table 17, show averages of 12.0 μ [range 10.8-12.8] and 12.4 μ [range 10.3-14.4] as the length of the inverted segment in two populations, corresponding to 79.8% [range 72.5-84.0%] and 78.0% [range 64.8-87.5%] of the average length of the short arm of chromosome 8. Ting [1958a, 1964] has reported an average length of 10.2 μ [range 8.8-13.0 μ] for the inverted segment or 62% [range 56.0-69.0%] of the average length of the short arm of chromosome 8. The variation shown by the two sets of measurements seem to indicate that there is no real differences between them. Besides, if it is considered the fact that the two sets of measurements were made under combinations of different factors [environment, material, methods of measurement, etc.] and that chromosome lengths vary according to the genotype and probably also to the environmental conditions, it is easy to understand the differences shown by the two studies.

The In9S has been found in teosinte populations from widely separated regions of Nobogame, Chihuahua in northern Mexico, Chalco in the highlands of the southeastern state of Mexico, and from Jutiapa in southern Guatemala. These findings confirm the previous reports of Ting [1958a, 1964, 1965]. The measurements made in the present study [Text Table 16] gave a variable length for the inverted segment, Nobogame teosinte having the longest and that of southern Guatemala the shortest. However, as discussed for the In1Lb and In8S, most probably these differences are not real but due either to sampling error, to racial effect, or to both. At any rate, they have lengths of the same order of magnitude. The same applies to any difference found between the present lengths and those reported by Ting [1958a, 1964, 1965]. Therefore, for the purpose of the present studies, the inversions on the short arm of chromosome 9 found in different populations will be considered as the same.

The teosinte populations of Nobogame, Chalco, and southern Guatemala do not have any geographical connection between them at the present time, and this isolation from each other probably has existed for thousands of years. If these widely separated populations possess in common the same inversion, e.g., the In9S, it seems to be good evidence supporting the idea that all teosintes, Mexican and Guatemalan, have evolved from a common ancestral population complex. Otherwise it has to be accepted that the inverted segment present in each population has been originated independently, which is very unlikely because the probability of the occurrence of two breakages at the same points in the same chromosome of different populations and their subsequent reunion to form the inversion is very low. Since the southern and northern Guatemala teosintes are related in this regard by the In1Lb inversion, then it further supports the above conclusion.

In the collections of the Nobogame teosinte studied, another inversion was found on the long arm of chromosome 1, here designated as In1La [the "a" means only that it was first observed during the present studies and serves to differentiate it from the In1Lb found later] [Plate IV, Figure 35].. The inverted segment of In1La probably is of the same actual length as that of the In1Lb [Text Table 15]. However, the former inversion differs from the latter in that a small knob is present within the inverted segment of In1La but absent from In1Lb. According to the length of the inverted segments and position on the long arm, it seems that both inversions can be considered as the same. One possibility is that In1La and In1Lb actually had the same common origin. After their separation into different populations of diverging lines, the inverted segment of that line giving origin to the Nobogame and related populations obtained the small knob from a homologous non-inverted segment through the occurrence of a rare two-strand double crossover. This possibility is increased because Nobogame teosinte has a small knob at the 1L1 position in relatively high frequency, but it is absent from the Guatemalan teosinte. Although this hypothesis is still speculative, it is worthy of consideration because it could be tested in two ways: 1] by actual experimental determination of whether the small knob can be transferred from the inverted to a non-inverted homologous segment; and 2] by searching and finding the same inversion without the knob in the Nobogame teo-

TABLE 18. Frequencies of different anaphase I configurations found in maize x teosinte and teosinte x teosinte F_1 hybrids examined and the expected percent pollen abortion due to the presence of heterozygous inversions.

	Number of Plants	No Bridge No Fragment	One Bridge One Fragment	Two Bridges Two Fragments [Indep.]	No Bridge One Fragment	Two Bridges Two Fragments [together]	Total Number Cells	Total Pollen Grains	Expected Aborted Pollen	Expected % Abortion
Maize x Nobogame teosinte										
17K	5	1837	83		3		1923	7692	172	2.2
18K	2	728	25		3		756	3024	56	1.8
24K	8	917	104	5	2	1	1029	4116	229	5.5
25K	4	912	54		2		968	3872	112	2.9
TOTAL	19	4394	266	5	10	1	4676	18704	569	3.0
Maize x Guerrero teosinte										
19K	5	269	1				270	1080	2	0.2
21K	6	407					407	1628	0	0.0
TOTAL	11	676	1				677	2708	2	0.07
Maize x N.Guatemala teosinte										
15K	9	1342	13		1	1	1357	5428	32	0.6
16K	8	801	4			1	806	3224	12	0.4
TOTAL	17	2143	17		1	2	2163	8652	44	0.5
Maize x S.Guatemala teosinte										
26K	5	406	40	1	3		450	1800	89	4.9
N.Guatemala teo. x Guerrero teo.	1	158	2				160	640	4	0.6
S.Guatemala teo. x Guerrero teo.	3	181	59	5	6		251	1004	145	14.4

as that of the other chromosomes. In the maize x Nobogame teosinte hybrid the presence of the In1La, In7L, In8S, and In9S heterozygous inversions tended to cause the asynapsis for variable lengths in the chromosome arm where these inverted segments were located. This non-pairing seems to occur more frequently about the location of the inverted segment [Plate VI, Figure 43]. A similar situation was observed for the In1Lb in the F_1 hybrid of maize x northern Guatemala teosinte [Plate IV, Figure 38]. In this latter cross, a probable small inversion was also detected about the $4L_1$ knob position [the large knob at the $4L_1$ position contributed by the maize parent served as the marker] since in 2 or 3 occasions a loop-like configuration was seen. However, the loops were not clear enough to be certain whether they were inversion loops or not. Nevertheless, a non-pairing of a segment about the knob was observed with relatively high frequency [Plate VI, Figure 44]. In regard to this $4L_1$ position it was also observed in the maize x Nobogame teosinte hybrid that even though the same large knob was in heterozygous condition the non-pairing of this region was not observed.

While these results show that frequent non-pairing of chromosomal segments at pachytene are not necessarily an indication that an inversion is present, nor do they means that it is always the effect of a heterozygous knob, these factors do sometimes cause regional asynapsis.

It is of importance to stress the fact that the inversions in teosinte populations were found to be knobless or at most include only a very small knob [e.g., In1La], and that the inverted segments are located at or near known knob positions. The In1La and In1Lb contain the $1L_1$ position, the In7L contains the $7L_1$ position. The In8S and the In9S comprise

TABLE 19. Observed frequencies of pollen abortion in maize x teosinte and teosinte x teosinte F_1 hybrids.

		P O L L E N						
Hybrid Progeny	Number of Plants	Starch Deficient Grains	Empty Grains	Deficient + Empty [Aborted]	Normal Grains	Total	Percent Sterility	Percent Fertility
Maize x Nobogame teosinte								
17K	2	116	35	151	6567	6718	2.2	97.8
18K	2	106	20	126	4884	5010	2.5	97.5
24K	4	595	69	664	13488	14152	4.7	95.3
25K	4	196	204	400	13472	13872	2.9	97.1
TOTAL	12	1013	328	1341	38411	39752	3.4	96.6
Maize x Guerrero teosinte								
19K	3	37	26	63	10071	10134	0.6	99.4
21K	2	39	12	51	5465	5516	0.9	99.1
TOTAL	5	76	38	114	15536	15650	0.7	99.3
Maize x N. Guatemala teosinte								
15K	3	301	8	309	9831	10140	3.0	97.0
16K	2	330	7	337	6303	6640	5.1	94.9
TOTAL	5	631	15	646	16134	16780	3.8	96.2
Maize x S. Guatemala teosinte								
26K	2	617	111	728	5511	6239	11.7	88.3
49K	3	956	377	1333	5362	6695	19.9	80.1
TOTAL	5	1573	488	2061	10873	12934	15.9	84.1
N. Guatemala teo. x Gro. teo.	1	101	8	109	3212	3322	3.3	96.7
S. Guatemala teo. x Gro. teo.	3	1483	1622	3105	9888	12993	23.9	76.1

segments of the short arm of chromosomes 8 and 9 which are closer to the ends of the arms. Knobs at the 8S and 9S positions are found in teosintes from Mexico and also from northern Guatemala. The 9S position also carries knobs in many maize populations from many regions in America. This observation is further substantiated by the same and other inversions found and previously reported by several investigators as given above in the review chapter on inversions. For example, Ting [1958a, 1964, 1965] has reported two inversions not observed in the present study, the In3L and the In5L. Both are knobless and located about the known knob positions $3L_1$ and $5L_1$. These observations seem to indicate that there is a negative correlation between the presence of inversions and the presence of knobs. That is, when an inversion is present, the knobs tend to be absent from the inverted segment, and the inversions tend to be absent in knobbed segments.

The results of the observations of cells at anaphase I are given in Text Table 18. Anaphase II configurations were not examined. The expected aborted pollen grains were calculated only from the anaphase I configurations observed based on the following assumptions. The no bridge-no fragment cells are expected to give rise only to fertile pollen grains; the one bridge-one fragment will produce 50% fertile pollen; those cells having two bridges-two fragments, but in independent bivalents, will give only 25% fertile pollen; the no bridge-no fragment should produce 50% fertile pollen; and finally the two bridge-two fragments in the same bivalent will give only aborted pollen grains. The results of these calculations are given in columns 10 and 11 of Text Table 18.

These data show that the least pollen abortion [less than 1%] was found in crosses of maize x Guerrero teosinte and maize x N. Guatemala teosinte. This probably indicates that in these two teosinte types the inversions are absent or infrequent. This conclusion seems to be confirmed by a single N. Guatemala teosinte x Guerrero teosinte hybrid examined which gave only 0.6% as expected pollen abortion due to inversions. This is also consistent with the finding of only one inversion [e.g., In1Lb] in N. Guatemala teosinte and none in Guerrero teosinte.

When this expected pollen abortion is compared with the observed pollen abortion determined by actual pollen grain counts [Text Tables 18 and 19], it is clearly shown that the degree of the observed pollen abortion is always higher than the expected one. This difference should also be expected because most plants of any variety under normal growing conditions, and even in the absence of any chromosomal aberration, always produce some pollen abortion due to the effect of unknown environmental factors and also to several types of accidental abnormal behavior of the chromosomes during microsporogenesis. An example of this is found in the progeny 21 K of a maize x Guerrero teosinte given in Text Table 18. According to these data, no abortion of pollen is expected due to inversions since, in 407 cells at anaphase I, none showed a bridge and a fragment characteristic of heterozygous inversions. Nevertheless, it was found 0.9% of pollen abortion in a total of 5516 pollen grains counted [Text Table 19]. At any rate the important point in this comparison is that the Guerrero teosinte behaves equally, whether it is crossed to maize or to northern Guatemala teosinte, showing that they are genetically very similar with respect to fertility in their hybrids in spite of their differences in knob constitutions.

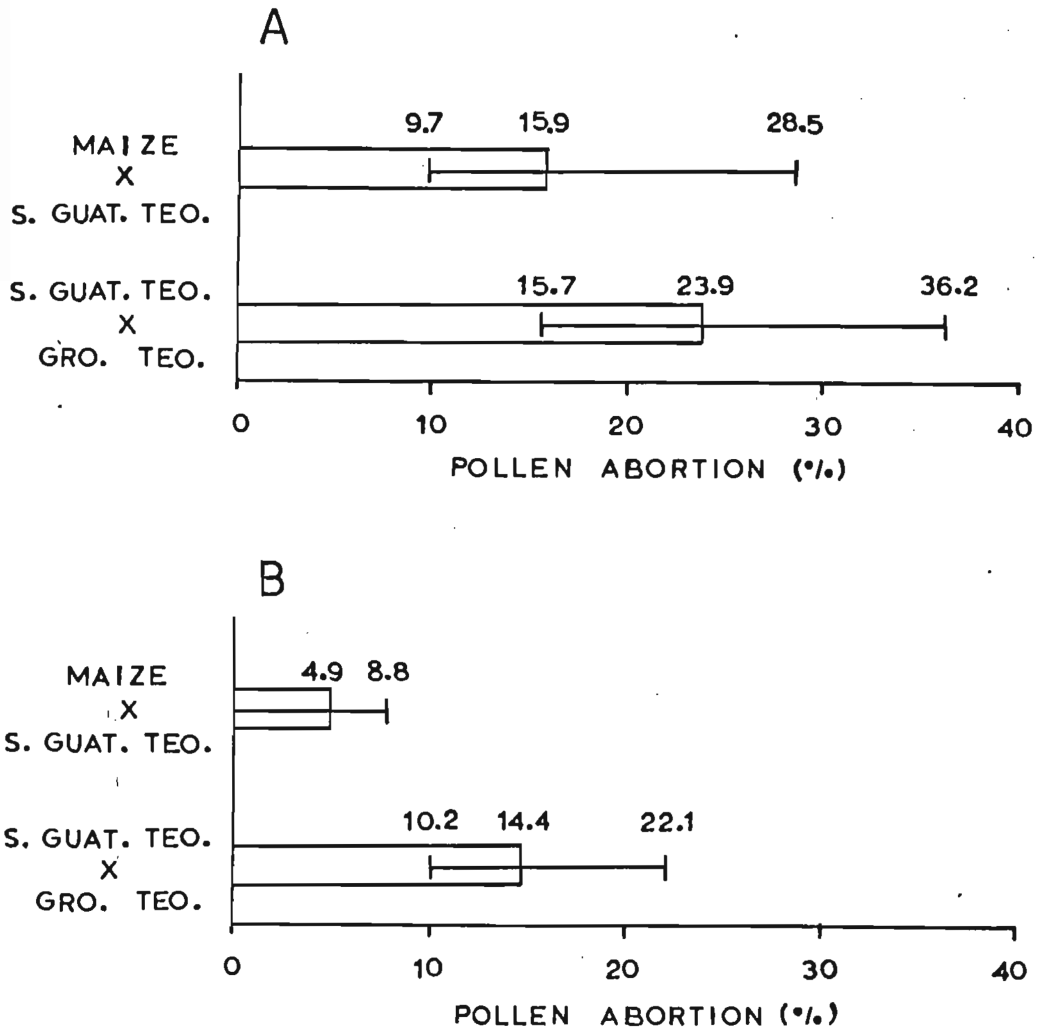

FIGURE 11. Average pollen abortion and their variability range in maize x southern Guatemala teosinte and southern Guatemala teosinte x Guerrero teosinte F_1 hybrids. A. Observed pollen abortion. B. Expected pollen abortion due to heterozygous inversions.

Similarly, when the maize x southern Guatemala teosinte and southern Guatemala teosinte x Guerrero teosinte hybrids are compared [Text Tables 18 and 19], it is found that both hybrids produce a high degree of pollen fertility. The average percent of pollen abortion both due to inversion heterozygosity and of total abortion apparently is higher in the S. Guatemala teosinte x Guerrero teosinte than in maize x S. Guatemala teosinte hybrids, but when the variability is considered, as shown in Text Figure 11, a large extent of overlapping exists, indicating that the difference found is not a real one. On the other hand, the difference in pollen abortion due to inversion heterozygosity between the same group of hybrids shows that there is considerable difference in the average percentage and also the ranges in the variation do not overlap. This indicates that the particular Guerrero teosinte used here in some unknown way may have induced the occurrence of a higher crossing over rate within the inverted segments in its hybrid with the southern Guatemala teosinte than than the maize inbred used did in a similar cross. Whether this kind of relationship is general for Mexican teosinte and for maize is not known, and further studies are needed for testing it by using a wider range of crosses.

The large differences between the expected and the observed percent pollen abortion in the maize x S. Guatemala teosinte and the S. Guatemala teosinte x Guerrero teosinte hybrids have been found to be due to a variable degree of asynapsis at pachytene. Even though the pachytene stage of the plants of these crosses appeared with very clumped chromosomes, it was possible to confirm in several cells that asynapsis was the cause and not due to desynapsis [Figures, 46, 47, and 48, Plate VI; Figures 52 to

TABLE 20. Frequencies of univalents found in microsporocytes at metaphase I in Guatemalan teosinte x Guerrero teosinte, and in maize x S. Guatemala teosinte.

CROSS	Number of univalents per cell							
	0	2	4	6	8	10	12	14
N. Guatemala x Guerrero								
27-7x17-1	261							
S. Guatemala x Guerrero								
14-1x24-11	150	55	8		1			
14-2x18-1	90	65	25	7	4	1		
14-4x23-10	33	44	30	7	4			
16-3x23-4	48	75	28	9	5	1		
Maize x S. Guatemala								
36K-2	26	98	66	24	4	3		
30K-2	38	113	85	46	11	4	1	
26K-10	35	104	33	3	1			
26K-1	107	128	65	8	3			
12K-6	31	117	154	79	43	11	1	1

56, Plate VII].

Counts of bivalents and univalents at metaphase I are given in Text Table 20. The results of these countings show that, in general, the pairing behavior between the homologous chromosomes in the S. Guatemala teosinte x Guerrero teosinte and the maize x S. Guatemala teosinte hybrids is similar. In both crosses, the 9 II + 2 I and 8 II + 4 I were the most frequent, and cells with higher numbers of univalents were less frequent. The single plant of N. Guatemala teosinte x Guerrero teosinte showed complete pairing of their homologous chromosomes as shown at the top line of Text Table 20. These facts again indicate that the Guerrero teosinte not only is similar to maize in chromosome morphology, but also in the synaptic behavior of their chromosomes with respect to those of the Guatemalan teosintes.

In the plants of maize x Nobogame teosinte hybrids studied, evidence was obtained for the presence of at least 4 heterozygous inversions as mentioned above [e.g., In1La, In7L, In8S, and In9S]. It is observed in Text Table 15 that the formation of characteristic configurations of heterozygous inversions is variable among different progenies from the same maize x Nobogame teosinte hybrid. As a consequence, the expected percentage of pollen abortion is very variable, ranging from 1.8 to 5.5% with an overall average of 3.0%. The observed overall average pollen abortion was 3.4% with a range from 2.2 to 4.7%. The similarity between the expected and the observed percentages seems to indicate that in these hybrids the main cause of pollen abortion was the presence of heterozygous inversions. The progeny 24K showed a larger percent of expected than observed pollen abortion. The only possible explanation for this anomalous situation seems to be found in the fact that, in several of the 8 plants studied for this progeny, a small number of cells at anaphase I were observed [less than 50] so that the sampling error could have been an important factor in increasing the expected percent pollen abortion over the observed one.

Maize populations. Similar to the case of teosinte, in the process of knob determinations in the maize collections analyzed for this study, the same In8S was observed in three collections, Guanajuato 21, Hidalgo 22, and Mexico 205. This finding confirms the previous observations of McClintock [1960] and of Kato [1964, 1966], who also found the same inversion in races of maize from the highlands of central Mexico and of South America.

The important point of these findings is that the same inversion occurs in both teosinte and maize populations from the same general area, the Central Mesa and the Bajio regions in Mexico.

Two possible interpretations can be offered: 1] this inversion is present in both maize and teosinte populations because it was already present in the ancestral population complex from which modern maize and teosinte diverged; and 2] maize populations showing the In8S inversion derived it from teosinte populations by introgressive hybridization. With the available information, it is not possible to discern which of the two is more probable, or whether there is some other possibility. More extensive research on this matter would be desirable to be carried on in the future.

Another point of interest in both maize and teosinte is the fact that apparently the inversions found in the present study, and those already reported in the literature, are present in populations of some regions and absent from populations of other areas. For example, the In8S has been found in teosinte populations from Nobogame, Durango, Guanajuato-Michoacan and Chalco regions, but absent from populations of the Balsas Basin and Guatemala. In maize, this inversion has been found in races from widely separated regions, e.g., genetic stocks of the United States, races of the highlands in Central Mexico, and of Bolivia in South America. The In9S was found in teosinte from Nobogame, Durango and Chalco regions in Mexico and from southern Guatemala. This same inversion is absent in teosinte from the Balsas Basin and northern Guatemala, as far as is known. Also, it has not been found, so far, in maize populations.

These facts seem to indicate that the inversions found in teosinte and maize are not distributed at random among populations of different regions, but some inversions are more widely distributed and others more restricted. This non-randomness of the inversion distribution parallels the situation found for the knobs at different positions. Moreover, many of the inversions tend to be knobless and located at or nearby the knob positions as mentioned above. This general parallelism between knobs and inversions seems to suggest that both have different adaptive values and the possibility exists that the inversions and the knobs may have alternative roles for accomplishing the same general function.

CHAPTER V

DISCUSSION

As was mentioned before, the problem of the origin and evolution of maize and teosinte is still controversial. Any solution will require different approaches using the techniques of several branches of the biological sciences. However, the major complexity seems to reside in finding a single approach that is acceptable to all. Whenever the data on a problem in biology still requires a phylosophical interpretation rather than an absolute analysis as with problems in physics and chemistry, then there will be honest differences in opinion. The present cytological work reported here has limitations because it is not based on direct evidence as would be the case for either an experimental approach or the discovery of the complete archaeological record. Consequently, in the present discussion general working hypotheses will be described which, in many respects, are speculative. Therefore, whenever possible the various alternative points of view will be compared.

That the chromosomes of maize and teosinte are, in general, similar to each other is known since their early cytological studies [Longley, 1937, 1938; and others].

In the present studies further evidences are given that maize and teosinte have similar genomes. This similarity as observed in pachytene chromosomes is shown by the general characteristics of chromosome morphology: the arm ratio and the chromomere pattern. Each chromosome of the genome has the same characteristics observed in either Mexican and Guatemalan maize or teosinte. The probability for more than one genome to evolve independently having chromosomes that match precisely regarding these two chromosome characteristics should be negligible. Consequently, the genomes of present day maize and teosinte populations must have had a common ancestry.

It is well known and here confirmed that all of the knobbed positions present in maize chromosomes have counterparts in the Mexican teosinte chromosomes. The reverse is not always true, since several positions having knobs in Mexican teosinte are not known in maize [Longley, 1937, 1938; Longley and Kato, 1965; Ting, 1958a, 1964, 1965; Kato and Blumenschein, 1967; McClintock, Blumenschein and Kato, unpublished; and others]. There is also evidence that knobs are conservative chromosomal structures. The chromosome morphology studies of many races from the highlands of Ecuador, Bolivia and Chile by McClintock [1959] have resulted in the finding that 2 small knobs, one in each of the long arms of chromosomes 6 and 7, were uniformly found in all the races studied. Two plants out of 125 examined were exceptional in that some additional knobs at other positions were present. Therefore, it seems more probable to consider that maize originated from teosinte than the other way. The origin of teosinte from maize would meet the difficulty of explaining how those knobs present in Mexican teosinte and absent in maize could have originated. The only chromosomal aberrations that have been found consistently in teosinte populations are inversions but since they are almost all knobless they would not be responsible for shifting of knob positions. Furthermore, when the many terminal knobs of the Guatemalan teosintes are considered, the difficulty becomes an impossibility because almost every distal segment of both arms of the chromosomes would need an inversion. The known inversions are intercalary with the exception of In8S and In9S which are subterminal. Intercalary knobs on the short arm of chromosomes 8 and 9 are not known in either maize or in teosinte. Also, so far as is known, many of the chromosome arms do not possess any inversions or, if they do, they are so small that their cytological observation is difficult. Furthermore, many chromosomes possess more than one knob position on a single chromosome arm, a fact that would require more than one inversion per arm. No indication of tandem or included types of compound inversions has so far been detected in maize and teosinte.

The geographical distribution of the knobs at different positions on the chromosomes of maize and teosinte is not at random. Populations of either maize or teosinte of different regions possess specific knob combinations, not only in regard to knob size and position, but also in frequency. As has been already suggested, these results indicate that different knob types possess different adaptive values. When these knobs were subjected to different selective pressures due to migration of populations into new regions, or to changes of the environment, new distribution patterns have resulted.

Two additional instances support the idea that knobs have an adaptive value. Knobs at several positions [e.g., $4S_2$, $5S_1$, and 7S] have been found in relatively high frequencies in teosinte populations of the Chalco region, but completely absent from maize populations of the same region. A similar situation is found in the Guatemalan teosintes that possess many terminal knobs, most of which are unknown in maize, not only from Guatemala but also from elsewhere. In both of these regions it is known that individuals of these species are constantly producing hybrids, many of them highly fertile, indicating that a possibility for reciprocal introgression occurs [Wilkes, 1967, 1972a]. However, the knob data indicate that in spite of this possibility many knobs are not introgressing from teosinte into maize populations. This means that there is a barrier for these knobs to introgress. Consequently, selection made by the farmers for the seed of their next planting must be in some way effective enough to avoid the introgression of at least the chromosomal segments carrying these knobs.

The regional knob distribution in both maize and teosinte could also be explained in certain cases by applying the concept of genetic drift. The migration of small populations could lead to loss or fixation by accident of one or more knobs. After they become established in a new environment, they can spread until they hybridize again restoring the original polymorphic condition. If the hybridizing populations happen to have lost or fixed some of the same knobs, they may produce various new combinations. This process described the situation when populations of whole regions present a knob polymorphism at every position. However, the genetic drift concept does not always explain the situation when certain knobs are absent from populations of a whole region, while the same knobs exist in a polymorphic condition in populations of adjacent regions. In this case, the occurrence of one of the two following events has to be assumed: 1] the whole region was colonized by the descendant populations of an original small one; or 2] the whole region was colonized by many small migrant populations and their subsequent generations which by random events have lost the same set of knobs. In the first case, since migration is considered between adjacent regions, the colonization of a region by a single migrant population is unlikely to occur because any one of the populations of the donor region can send a series of migrations into the recipient region over long periods of time. If this is accepted, then the probability for all the migrant populations, considered in space and time, to lose or fix the same set of knobs would be negligible. From this improbability, the occurrence of the second event as given above also becomes unlikely, if not impossible.

The second fact which suggests that the knob distribution patterns have various adaptive values has already been given above when maize and teosinte populations from the same regions were compared. It is difficult to visualize how genetic drift can maintain several knobbed segments in teosinte populations without introgressing them into maize if hybridization is occurring constantly.

Nevertheless, genetic drift might be important in effecting changes in knob constitutions of local, small and isolated populations in teosinte and maize.

If it is accepted that knobs possess different adaptive values, then the non-random knob distribution patterns found in teosinte populations at the regional level can be interpreted as follows. In the past, an ancestral population complex existed that was polymorphic for all the knobs found in the existing teosinte populations. The ancestral populations, after becoming widely distributed by the process of migration to new regions, became subjected to different sets of selective forces due to changing environmental conditions so that the knob combinations were adjusted according to the balance of the gene pool of the populations under different selection pressures. In this way, those complexes better coadapted to the new conditions were selected out of the original knob polymorphism. This, in turn, would imply that the regional differences in knob composition found at present are the reflection of past changes that occurred in the expanding ancestral population complex, and the variation found within any given region would represent adjustments that occurred in a more recent past, or are occurring at the present time because of variations in the local environments.

The experimental studies of the abnormal chromosome 10 and B chromosomes reviewed earlier in this paper have disclosed the fact that these unusual chromosomes affect the recombination rate in various ways, depending upon whether or not the chromosome region in question is associated with a knob. Also, it has been found that knobs, especially when heterozygous, reduce the amount of crossing over in segments adjacent to them and further this reduction has an inverse relation to knob size. These results indicate that knobs are not inactive or neutral chromosomal structures, and that directly or indirectly they are contributing to the important function of controlling recombination rate.

Dobzhansky [1952, p. 222] has stated that "....adaptively integrated polygene complexes can be maintained in cross-breeding populations with the aid of genetic mechanisms other than chromosomal inversions. Any factor which restricts or prevents crossing over in chromosomes, or parts of chromosomes, can accomplish the same biological function...the genes carried in the sections [with reduced crossing over]...are inherited in blocks. Such gene blocks may act exactly as gene complexes bound together by inversions". Grant [1964] defined the concept of supergenes as "different genes which are not necessarily similar functionally, but which cooperate to produce some adaptive characteristic, are sometimes tightly linked and inherited as a block". That these gene complexes have adaptive values have further been considered by Grant [1964], Mayr [1970], Dobzhansky [1970], Stebbins [1971] and Ford [1971], who give many examples of supergenes found in natural populations of animal and plant species.

If this concept of the "supergene" and the way it can be developed is applied to the knobs, it seems clear how they can get a variable adaptive value. When a large intercalary knob is in a heterozygous condition, especially with a knobless segment, the homologous synaptic condition is not achieved and crossing over is reduced or suppressed between the segments adjacent to the knob and the corresponding homologous segment of its knobless counterpart. If this kind of pairing is frequent in the populations, and occurs over long periods of time, then the segments with reduced recombination rate will tend to accumulate different allelic combinations so that selection can act upon them. With different knob combinations, it would be possible to develop supergenes of various magnitudes giving further opportunities for selection to act.

Since many small inversions have been found in populations of teosinte and also in maize, which tend to be knobless and located at or near known knob positions, there is a further possibility for supergene development in the chromosomes of these species. This is especially true in the cases of Chalco and Guanajuato teosintes where inversions coexist with homologous non-inverted and knobbed segments. However, the presence of many inversions in populations with a predominance of knobless chromosomes like Nobogame teosinte would be important. In these cases, the inversions could take the place of the knobs as centers for supergene formation. The blocks of genes would control the genetic variability of the population which then could cope with changes in the selective pressures such as that between man and nature.

As already discussed above, some knobs have been found to be restricted in teosinte populations growing in close sympatry with maize populations indicating no introgression of these knobs. However, in the case of other knobs, the possibility that they are introgressing between maize and teosinte populations could not be ruled out with certainty. These results therefore could be interpreted in two possible alternative ways: 1] teosinte and maize populations are genetically isolated from each other in spite of the constant formation of fertile hybrids; and 2] some segments of both species are not introgressing and others are able to do so.

The concept of coadaptation of gene complexes refers to the harmonious function of the gene components within a complex and with other genes or gene complexes present in the population, giving rise to an adaptively valuable phenotype [Dobzhansky, 1970]. Also Mayr [1970] has stated that "since the primary gene action in multicellular organisms is usually several steps removed from the peripheral phenotypic character, it is obvious that non-pleiotropic genes must be rare if they exist at all". If some knobs are unable to introgress from teosinte into maize, this would mean that the supergenes linked to these knobs have not become coadapted to the maize genetic background. Consequently, they are eliminated from maize because they would produce phenotypes unfit to artificial selection through which maize survives. Also, if the adaptiveness of these knobs depends upon a mutual coadaptation with other genes and gene complexes through pleiotropic effects, then it seems possible that many of the knobs of either maize or teosinte should be unable to introgress from one species to the other.

A selection experiment to develop reproductive isolation between two populations of maize was conducted by Paterniani [1969]. The selection made was against intercrossing. Starting with about 40% original intercrossing, this was reduced to about 4% in six generations of selection. This experiment has demonstrated that, with strong selection pressure against intercrossing, an assortative type of fertilization is developed and the two populations tend to become isolated. A similar situation must be occurring between sympatric teosinte and maize populations through the artificial and the natural selection operating upon them. That an assortative type of fertilization occurs in these populations has been reported by Castro [1970] who has found that when a mixture of equal amounts of teosinte and maize pollen is used for pollinating maize silks, the teosinte pollen does not compete well with maize pollen in effecting fertilization. This kind of isolating mechanism must be important under natural conditions for preventing introgression which is further strengthened by the disruptive selection acting between the species. It would be important to undertake further investigations in this regard and find out whether the pollen of the F_1 hybrids compete better or worse with either maize or teosinte pollen. The results of this type of investigation will show with what frequency the backcrosses of the hybrids to either parent occur in nature, an information that is important to clarify the genetic relationships between sympatric partners of maize and teosinte.

Another important study on this same general subject that should be done in the future is to find out how effective is artificial selection, as practiced by native farmers in those places where teosinte and maize grow sympatrically, in preventing the introgression from teosinte into maize. The use of knobs as markers seems to be advantageous because, through the same investigations, the possibility exists to find out whether knobs can show various adaptive values or not. The inversions could also be used for the same purpose.

CHAPTER VI

SUMMARY

Extensive studies on chromosome morphology of maize populations from all over the Americas have resulted in the main conclusion that modern maize populations were derived from the admixture of several ancient maize germplasms. These germplasms developed in several localities by independent domestication from the wild ancestor, which already was differentiated into various distinct racial types.

These studies suggested that a similar approach in both teosinte and maize might provide further insights into their origin and evolution.

A comparative study of teosinte and maize pachytene chromosome morphology was undertaken from three different aspects: 1] the basic characteristics of length, arm ratio, chromomere distribution, and knob position and size; 2] the knob frequency distribution in teosinte collections from its whole distribution range in Mexico and Guatemala, and maize collections from central Mexico; and 3] the presence of small inversions in teosinte chromosomes from different regions.

The results of these studies are:

1. The length of the corresponding teosinte and maize chromosomes does not show differences at the species level, although differences at the racial level may exist.

2. No differences in arm ratios were found between chromosomes of teosinte and maize genomes.

3. There are many similar chromosome segments between maize and either the Mexican and the Guatemalan teosintes in regard to the chromo-

mere distribution.

4. Maize and Mexican teosinte are more similar since they have mostly intercalary knobbed positions. Many of these are common to both species and their knobs were found in similar overall frequencies. However, Mexican teosintes possess more knobbed positions than maize.

5. Contrary to the above situation, the Guatemalan teosintes are different, in that they possess exclusively terminal knobs on both the long and the short chromosome arms. However, the differences are not absolute since several knobs are present in common positions on the chromosomes of maize and of Mexican and Guatemalan teosintes. Futhermore, knobless chromosomes are present in populations of the two species.

6. Knobs at different positions on the chromosomes of teosinte populations are not distributed at random, but follow certain patterns. There are knobs at several positions that have shown a generalized distribution pattern, while knobs at other positions had more restricted distribution patterns. In regard to the knob size, it was found that populations of different regions may possess a predominance of knobs with different sizes or be knobless. Consequently, populations having a unique knob combination are found in different regions.

7. When two or more knob positions on the same chromosome or chromosome arm are considered together, three situations occur: a] knobs at one position prevail in a given region while those of the other position are absent, and the reverse may be found in other regions; b] knobs at the two positions occur in populations of the same region; and c] a combination of a] and b].

8. In general, a similar situation was found among maize populations

in regions and races of central Mexico.

9. Many knobs have been found existing in high frequencies in teosinte, but absent in sympatric and hybridizing maize populations. Some of these knobs, however, are present in high frequencies in maize from regions where no teosinte exists at present.

10. Two types of abnormal chromosome 10 [type I and II] were found in teosinte, but each type in populations from different regions. Only the type I abnormal chromosome 10 exists in maize populations, and they are coexisting in close sympatry with teosinte populations possessing either type of abnormal chromosome 10.

11. B chromosomes in maize and Mexican teosinte have similar morphology. This chromosome type was not found in Guatemalan teosintes.

12. Several inversions already reported in the literature, and two new ones [e.g., paracentric inversions on the long arms of chromosomes 1 and 7], causing a low frequency of pollen abortion, were found in teosinte plants. The same inversions are present in widely separated populations without any present-day geographical connections between them.

13. The known naturally occurring inversions in teosinte and maize populations are knobless, or small knobbed, and usually located at or near known knob positions.

The above results have led to the following conclusions and interpretations:

1. Both species possess the same basic genome. Consequently all existing teosinte populations are derivatives of a common ancestor, and maize must have originated from a teosinte population complex similar to the existing Mexican teosinte. This interpretation is further supported

by the presence of the same inversions in isolated populations.

2. The several knob types at different positions possess various adaptive values. Also, knobs at different positions on the same chromosome have either or both compensatory and complementary effects. No evidence exists of a knob shifting mechanism in teosinte and maize chromosomes. Consequently, the existing populations of both species are derivatives of a common ancestral population complex which had all the knobbed positions known at present. Furthermore, different selection pressures that acted upon the many knob combinations in space and time in the past brought about the non-random distributions observed at present.

3. There are many chromosomal segments carrying knobs that are not introgressing from teosinte into maize, a fact that strengthens the idea that different knobs possess various adaptive values. Whether all chromosome segments of the genome behave similarly is not known, and further research is needed to clarify this point.

4. The several inversions found might possess different adaptive values and be knob substitutes for accomplishing the same evolutionary role.

5. Based on the fact that knobs reduce recombination rate in the segments carrying them, the possibility is proposed and discussed that knobs, depending upon their size and location, favor the development of different supergenes, acquiring in this way various adaptive values.

6. It is further discussed that the process of genetic drift is not adequate for explaining all the results obtained in the present studies.

CHAPTER VII

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APPENDIX

TABLE 1. General information of the collections of teosinte from Mexico and Guatemala used in the present studies.

No. on Map	Collection Designation	Altitude m.	Collection Place
	MEXICO		
1	Nobogame	1850	Nobogame, Chihuahua
2	Nobogame Wilkes 1964	1850	Nobogame, Chihuahua
3	K-69-2	1700	Manuel Doblado, Guanajuato
4	K-69-10	2100	Moroleón-Pinícuaro, Gto.
5	K-69-11	2150	Pinícuaro, Guanajuato
6	K-69-1	1710	Manuel Doblado, Guanajuato
7	K-69-7	1925	Uriangato-Moroleón, Gto.
8	K-67-7	1560	Km.48 Iguala-Teloloapan, Gro.
9	K-67-9	1620	Km.11 Teloloapan-Arcelia, Gro.
10	K-67-12	1130	Km.47 Teloloapan-Arcelia, Gro.
11	K-67-8	1570	Km.52 Iguala-Teloloapan, Gro.
12	K-69-13	1350	Mazatlán, Guerrero
13	Beadle-'72	1100	El Salado [3Km. East Mazatlán], Gro.
14	Beadle-'72	1100	" " "
15	Beadle-'72	1100	" " "
16	47711, Wilkes '63	1510	Ranchos Nuevos, Guerrero
17	47335, Wilkes '63	1350	Mazatlán, Guerrero
18	K-65-2	±2200	Miraflores, México
19	K-66-1	±2300	Ozumba, México
20	K-67-1	2250	Temamatla, México
21	K-67-2	2470	Juchitepec, México
22	K-68-1	±2400	San Antonio Tecomi-Milpa Alta, D.F.
23	K-68-2	±2300	San Mateo, Distrito Federal
24	K-68-6	±2300	Zoquiapan, México
25	K-69-12	±2300	San Francisco Acuautla, México
26	K-67-3	2320	Tepetlixpa, México
27	K-68-4	2260	Chalco, México
28	1970, T-1	±2400	Tlalmanalco, México
29	1970, T-2	2260	Chalco, México

TABLE 1. [continued]

No. on Map	Collection Designation	Altitude m.	Collection Place
30	1970, T-3	2340	Miraflores-Tlalmanalco, México
31	1970, T-4	2250	Xochimilco, D.F.
32	K-67-17	1390	Km.116 Toluca-Tejupilco-Luvianos, Méx.
33	K-67-18	1371	Km.151 " " " "
34	K-67-19	1490	Km.168 " " " "
35	K-67-21	1185	Km. Toluca-Valle Bravo, Tingambato,Méx.
36	K-67-16	1410	Km.112 Toluca-Tejupilco-Luvianos, Méx.
37	K-67-20	1110	Km.175 Toluca-Valle Bravo - Tingambato, México
38	K-69-4	1900	Villa de Jiménez, Michoacán
39	K-69-6	1800	Copándaro-Chucándiro, Michoacán
40	K-69-8	2000	Puruándiro, Michoacán
41	K-69-9	2000	Puruándiro, Michoacán
42	K-69-3	1800	Churintzio, Michoacán
43	K-69-5	1800	Chucándiro, Michoacán
44	45470 Wilkes	1950	Los Espinos, Michoacán
45	K-67-14	820	Km.43 Huetamo-Morelia, Michoacán
46	K-67-13	800	Km.24 Huetamo-Morelia, Michoacán
47	47942 Wilkes	600	Huetamo, Michoacán
48	47890 Wilkes	700	Cerro Huetamo, Michoacán
49	K-67-15	1000	Km.127 Huetamo-Morelia, Michoacán
50	K-67-23	1040	Km.27 Tingambato-Tuzantla, Michoacán
51	K-67-25	1235	Km.37 Zitácuaro-Tuzantla, Michoacán
52	K-67-24	880	Km.46 Zitácuaro-Tuzantla, Michoacán
53	48897 Wilkes		Ciudad Hidalgo, Michoacán
54	48085 Wilkes		Queretanillo, Michoacán
	GUATEMALA		
55	51850 Wilkes		El Amatillo, Chiquimula
56	51839 Wilkes		Cuesta de Gracia, Jutiapa

TABLE 1. [continued]

No. on Map	Collection Designation	Altitude m.	Collection Place
57	51764 Wilkes		Buenavista, Jutiapa
58	Cutler 202A		Jutiapa
59	Wilkes		San Antonio Huixta, Huehuetenango
60	Wilkes		Tzisbaj, Huehuetenango
61	Wilkes		Monajil, Huehuetenango

TABLE 2. General information on the collections of maize from central Mexico used in the present studies. The collections marked with an asterisk are those in which knob data were already used by McClintock, Blumenschein and Kato [unpublished].

No. on Map	Collection Number		Collection Place	Altitude m.	Racial Classification
1	Guanajuato	2	San Nicolás, Mpio. León	1885	Cónico
2		3	Ejido San Juan, Irapuato	1722	
3		10	Celaya	1808	
4		16	La Estancia, Irapuato	1722	Pepitilla
5		21	Juventino Rosas		C. Norteño-Pepitilla
6		24	Dolores Hidalgo	1987	Cónico Norteño
7		28	Comonfort		
8		30	Cuerámaro		C. Norteño-Chalqueño
9		36	Salvatierra	1749	
10		42	Celaya	1808	
11		51	San Miguel Allende	1855	Cónico Norteño
12		69	Cortazar	1808	C. Norteño-Tuxpeño
13		71	Yuriria		Celaya-Cónico
14		91	San Luís de la Paz	2020	
15		100*	El Sotelo, León	1828	Maíz Dulce
16		101*	Irapuato	1828	Celaya
17		102*	El Sotelo, León	1828	Cónico Norteño
18	Guerrero	3*	Iguala	731	Pepitilla
19		4*	Municipio Huitzuco		Pepitilla
20		6*	Iguala	731	Pepitilla
21		8*	Atenango del Río	730	Pepitilla
22		9*	Huamuztitlán		Pepitilla
23		36*	Coyuca de Catalán	210	Vandeño-Cónico
24		39*	Coyuca de Catalán	210	Vandeño
25		60	Arcelia	420	Olotillo
26		77*	Teloloapan	1700	Pepitilla
27		96	Petatlán	50	
28		99	El Ocote [N. de Petatlán]	180	Reventador

TABLE 2. [continued]

No. on Map	Collection Number		Collection Place	Altitude m.	Racial Classification
29	Guerrero	106	Puerto del Aguila, Petatlán	840	Reventador
30		134*	Murga	100	Vandeño
31		150*	Tierra Colorada	300	Vandeño
32		153*	San Jeronimo	30	Vandeño
33		166*	San Marcos	50	Vandeño
34		200	Troncones, Mpio. La Unión	10	Vandeño
35		208	Coahuayutla	590	Vandeño
36		210*	Agua de Correa, Petatlán	80	Vandeño-Olotón
37		212*	El Pintero, Mpio. Galeana		Vandeño
38		217	La Unión	60	Reventador
39		221*	Tierra Colorada, Iguala		Pepitilla
40		222	Cacahuamilpa		Maíz Ancho
41		225	Acuitlapán		Maíz Ancho
42		228	Lo de Tapia, Taxco		Maíz Ancho
43		B-1a	El Salado, Mazatlán	1100	Vandeño
44		B-1b	El Salado, Mazatlán	1100	Vandeño
45		B-2	El Salado, Mazatlán	1100	Vandeño
46		B-3	El Salado, Mazatlán	1100	Vandeño
47	Hidalgo	5	Actopan	2050	Marceño
48		13	Sacualtipán	1700	Chalqueño-Celaya
49		18	Actopan	2050	
50		22	Acaxochitlán	1600	Cónico
51		26	Zapotlán de Juárez	2200	
52		33	Huejutla	200	Tabloncillo-Tuxpeño
53		34*	Metztitlán	1650	Cónico-Pepitilla
54		37	Metztitlán	1400	Tuxpeño-Chalqueño
55		41*	Texcalera Molango	1600	Chalqueño-Pepitilla
56		46	Ixtlahuaca	1500	Celaya
57		49	Lolotla Cuitchapa	1700	Elotes Occidentales
58	Mexico	3	México-Toluca Km. 57	2655	Cónico

TABLE 2. [continued]

No. on Map	Collection Number		Collection Place	Altitude m.	Racial Classification
59	Mexico	7*	México-Toluca Km. 60	2655	Cacahuacintle
60		7A*	Toluca [Market]	2655	Cacahuacintle
61		33	Chalco	2260	
62		34	Chalco [field with teosinte]	2260	
63		36*	Tepotzotlán		Marceño
64		38	Huehuetoca		Celaya-Pepitilla
65		46	San Felipe del Progreso		Chalqueño
66		49	Ixtapaluca		
67		51	Tlalmanalco		
68		59	Metepec		
69		62	Ozumba		
70		74	Amecameca		
71		77	Tenango del Valle	2620	
72		95	Amanalco de Becerra	2380	Cónico-Chalqueño
73		142*	Coscomate del Progreso, Jilotepec		
74		181	Timilpan		Palomero-Arroceño
75		182	Chapa de Mota		Cónico
76		205	Temascaltepec		
77		207*	Toluca	2655	Cónico
78		208*	Chalco	2280	Chalqueño
79		210*	Santa Mónica		Palomero Toluqueño
80		211*	Toluca	2655	Palomero Toluqueño-Cónico
81		225	La Puerta de Santiago		Maíz Ancho
82		M-1	Tlalmanalco		
83		M-2	Chalco	2260	
84		M-3	Miraflores-Tlalmanalco	2340	
85	Michoacan	40	San Miguel Ocurio, Zitácuaro		
86		41	Ciudad Hidalgo		Pepitilla
87		45	Zacapu	1986	Chalqueño
88		54	Yurécuaro		Argentino

TABLE 2. [continued]

No. on Map	Collection Number		Collection Place	Altitude m.	Racial Classification
89	Michoacán	74	Zamora	1564	
90		78*	Coyacho		Pepitilla
91		79*	Tangancícuaro		Pepitilla
92		105*	Tiquicheo	340	Tuxpeño-Chalqueño
93		186*	Huandacareo		
94		191*	Churintzio		
95		199	Tingambato	1000	Chalqueño-Pepitilla
96		200*	Tingambato	1000	Tuxpeño
97		204	Purépero		Chalqueño-Pepitilla
98		211	Senguio		
99	Morelos	1*	Jojutla	885	Pepitilla
100		3*	Jojutla	885	Pepitilla
101		13*	Jiutepec, E. Zapata	1190	Pepitilla
102		14*	Municipio Tetecala	1000	Pepitilla
103		15*	Zacatepec	854	Pepitilla
104		17*	Paraimalco		Pepitilla
105		18*	Jojutla	885	Pepitilla
106		19	Tlalquitenango		Pepitilla
107		22	Jonacatepec		Pepitilla
108		27	Yecapixtla		Maíz Ancho
109		60	Tlayacapan		Maíz Ancho
110		79	Temixco		Maíz Ancho
111		93	Tetlama		Maíz Ancho
112	Puebla	33	Huejotzingo		Cónico-Palomero Toluqueño
113		196*	Tehuitzingo	1150	Pepitilla
114		200*	Chinantla	1100	Pepitilla
115		219*	Chiautla de Tapia	1010	Pepitilla
116		223*	Chietla	1100	Pepitilla
117		229*	Tecomatlán	1000	Pepitilla
118	Querétaro	1	San Juan del Río	1800	Pepitilla

TABLE 2. [continued]

No. on Map	Collection Number		Collection Place	Altitude m.	Racial Classification
119	Querétaro	4	Pedro Escobedo		
120		15	Santa Rosa de Jáuregui	2000	Celaya
121		20*	Huimilpan	2300	Cónico Norteño
122		29	Amealco	2450	Cónico Norteño
123		31	Tequisquiapan	1800	Cónico Norteño
124		34	Cadereyta	2032	Cónico Norteño
125		39	Colón	2300	Celaya-Chalqueño
126		43	Tolimán	1500	
127		48*	Pinal de Amoles	2300	Celaya-Chalqueño
128		49	Pinal de Amoles	2300	Cónico Norteño
129		50*	Conca	500	Tuxpeño
130	S.L. Potosí	12*	Xilitla	1037	C. Norteño-Tuxpeño
131		78*	Obregón, Mpio. de Rayón	1155	Tuxpeño
132		95*	Tampamolón Corona	200	Tuxpeño-Xmehenal
133		128*	Tamazunchale	210	Tuxpeño-Olotillo
134		150*	Potrero Grande, Cárdenas	1200	
135	Tlaxcala	1*	Calpulalpan		Cónico
136		3*	Huamantla		
137		5	Amaxac	2200	Cacahuacintle
138	Veracruz	215*	Tempoal	100	Tuxpeño

TABLE 3. Frequencies for the different knob sizes of the 1S2, 1L1, 2S1, 2L1, 3S1, 3L1, 4S2, and 4L1 knob positions found in each of the maize collections from regions of central Mexico. The first column, number on map, refers to the numbering of the collections in the collection distribution map given in the text. The small letters l, m, s, and o, indicate large, medium, and small knob sizes and the knobless condition respectively. Knob frequencies marked with an asterisk indicate that the total number of chromosomes examined was less than the one given in the rightmost column.

No. on Map	COLLECTION NUMBER		CHROMOSOME KNOB POSITION AND SIZE																														TOTAL NUM. CHROM.
			1S2				1L1				2S1				2L1				3S1				3L1				4S2				4L1				
			l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	
1	GUANAJUATO	2	0	2	1	7	1	1	2	6	0	2	2	6	3	0	0	7	0	0	0	10	5	1	0	4	0	0	0	10	4	2	0	4	10
2		3	2	3	0	7	0	0	0	12	2	1	0	9	11	0	0	1	0	0	0	12	10	0	0	2	0	0	0	12	12	0	0	0	12
3		10	8	1	0	3	0	2	0	10	0	3	0	9	10	0	0	2	0	0	0	12	7	2	0	3	0	0	0	12	10	1	0	1	12
4		16	1	1	0	4	0	0	0	6	0	0	0	6	3	1	0	2	0	2	0	4	6	0	0	0	0	0	0	6	4	0	0	2	6
5		21	0	3	0	5	0	3	0	5	0	0	0	8	6	0	0	2	3	0	0	5	6	0	0	2	0	0	0	8	4	0	0	4	8
6		24	4	2	0	4	1	2	0	7	5	1	0	4	6	1	0	3	0	0	0	10	7	1	0	2	0	0	0	10	9	0	0	1	10
7		28	3	4	0	3	0	1	0	9	8	0	0	2	6	0	0	4	0	0	0	10	0	5	0	5	0	0	0	10	8	1	0	1	10
8		30	1	2	0	5	0	0	0	8	3	1	0	4	5	0	0	3	0	2	0	6	6	0	0	2	0	0	1	7	6	0	0	2	8
9		36	1	5	0	6	0	0	0	12	2	2	0	8	8	2	0	2	0	0	0	12	4	2	0	6	0	0	0	12	10	0	0	2	12
10		42	5	2	0	5	0	2	0	10	8	0	0	4	2	3	0	7	1	2	0	9	8	1	0	3	0	0	0	12	7	2	0	3	12
11		51	2	4	1	3	0	0	0	10	7	0	0	3	8	0	0	2	1	0	0	9	1	5	0	4	0	0	0	10	9	0	0	1	10
12		69	1	3	1	5	0	0	0	10	0	0	0	10	7	0	0	3	0	0	0	10	2	0	0	8	0	0	0	10	8	0	0	2	10
13		71	7	1	0	4	0	0	0	12	0	0	0	12	7	0	0	5	0	0	0	12	8	1	0	3	0	0	0	12	9	0	0	3	12
14		91	6	2	0	2	1	1	0	8	5	1	0	4	4	0	0	6	0	0	0	10	6	0	0	4	0	0	0	10	10	0	0	0	10
15		100	10	0	1	1	0	0	0	12	2	0	0	10	12	0	0	0	0	5	0	7	12	0	0	0	0	0	0	12	11	0	0	1	12
16		101	4	6	11	11	0	0	0	32	5	2	0	25	15	13	1	3	0	2	0	30	8	16	2	6	0	0	0	32	22	10	0	0	32
17		102	3	4	0	3	0	0	0	10	6	0	0	4	4	0	0	6	0	0	0	10	10	0	0	0	0	0	0	10	10	0	0	0	10
18	GUERRERO	3	0	3	0	3	0	0	0	6	0	0	0	6	0	2	0	4	0	0	0	6	0	1	0	5	0	0	0	6	1	2	0	3	6
19		4	1	0	0	7	0	0	1	7	0	1	0	7	2	2	0	4	0	0	0	8	3	1	0	4	0	0	0	8	6	0	1	1	8
20		6	2	3	1	4	0	0	0	10	0	0	0	8*	1	0	0	7*	0	0	0	10	2	0	0	8	0	0	0	8*	8	0	0	0*	10
21		8	0	0	0	4	0	0	0	4	0	0	0	4	0	0	0	4	0	0	0	4	3	0	0	1	0	0	0	4	4	0	0	0	4
22		9	1	2	0	3	0	0	0	6	1	0	0	5	0	1	0	5	0	0	0	6	6	0	0	0	0	0	0	6	6	0	0	0	6
23		36	0	6	2	4	0	0	1	11	0	5	0	7	0	11	0	1	0	0	0	12	1	8	0	3	0	0	0	12	7	5	0	0	12
24		39	0	0	4	6	0	0	0	10	0	3	3	4	0	8	1	1	0	0	0	10	1	1	2	6	0	0	0	10	7	0	1	2	10
25		60	4	1	0	7	0	0	0	12	0	0	0	12	11	0	0	1	2	0	0	10	3	0	0	9	0	0	0	12	10	0	0	2	12
26		77	4	1	0	1	0	0	0	6	0	0	0	6	1	1	0	4	0	0	0	6	0	1	0	5	0	0	0	6	3	0	0	3	6
27		96	5	3	1	1	0	1	1	8	0	0	0	10	1	8	0	1	0	0	0	10	5	2	0	3	0	0	0	10	6	3	0	1	10
28		99	0	3	0	3	0	0	0	6	0	0	0	6	3	2	0	1	0	0	0	6	0	4	0	2	0	0	0	6	4	2	0	0	6
29		106	0	0	2	8	0	0	2	8	0	0	0	10	3	6	0	1	0	0	0	10	5	2	0	3	0	0	0	10	5	2	0	3	10
30		134	0	0	4	6	0	0	0	10	0	0	0	10	7	2	0	1	0	0	0	10	2	6	0	2	0	0	0	10	8	2	0	0	10
31		150	0	9	0	3	0	0	1	11	0	0	0	12	0	2	2	8	0	0	0	12	2	3	0	7	0	0	0	12	5	5	1	1	12
32		153	0	4	1	7	0	0	0	12	0	0	0	12	6	3	0	3	0	2	0	10	5	6	0	1	0	0	0	12	5	4	0	3	12
33		166	0	4	2	0	0	3	0	3	0	2	0	4	0	5	0	1	3	1	0	2	5	1	0	0	0	0	0	6	0	6	0	0	6
34		200	2	2	3	5	0	0	1	11	0	0	0	12	8	1	1	2	0	0	0	12	3	3	1	5	1	1	0	10	8	3	0	1	12
35		208	3	1	1	5	0	0	0	10	0	0	0	10	8	1	0	1	0	0	0	10	0	3	0	7	0	0	0	10	3	1	1	5	10
36		210	0	8	0	0	0	0	0	8	0	1	1	6	0	7	0	1	0	0	0	8	4	4	0	0	0	0	0	8	7	0	0	1	8
37		212	0	1	3	8	0	0	0	12	0	0	0	12	2	8	2	0	0	0	0	12	4	7	0	1	0	0	0	12	2	8	0	2	12
38		217	3	4	0	3	0	0	0	10	0	0	0	10	4	3	0	3	0	0	0	10	4	2	0	4	2	2	0	6	6	1	0	3	10

TABLE 3 (Continued).

NO. CN MAP	COLLECTION NUMBER	CHROMOSOME KNOB POSITION AND SIZE																																TOTAL NO. CHROM.
		1S2				1L1				2S1				2L1				3S1				3L1				4S2				4L1				
		l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	
39	GUERRERO 221	6	5	0	7	0	0	0	18	0	0	0	18	10	1	0	7	0	0	0	18	3	0	1	14	0	0	0	18	15	1	0	2	18
40	222	5	2	0	5	0	0	0	12	0	0	0	12	4	0	0	8	0	0	0	12	5	0	0	7	0	0	0	12	10	1	0	1	12
41	225	5	1	0	4	0	0	0	10	3	0	0	7	1	1	0	8	0	0	0	10	4	0	0	6	0	0	0	10	9	0	0	1	10
42	228	3	3	0	4	0	0	0	10	1	0	0	9	4	1	0	5	0	0	0	10	4	0	0	6	0	0	0	10	8	0	0	2	10
43	Beadle 1a	9	8	0	17	0	0	0	34	4	0	0	30	27	0	0	7	0	0	0	34	5	7	0	22	0	0	0	34	30	0	0	4	34
44	Beadle 1b	5	13	1	23	0	0	0	42	3	0	3	36	18	6	0	18	0	0	0	42	4	9	0	29	0	1	0	41	39	0	0	3	42
45	Beadle 2	3	10	1	20	0	0	0	34	2	1	0	31	9	2	0	23	0	0	0	34	3	2	0	29	0	0	0	34	17	7	0	10	34
46	Beadle 3	4	5	0	5	0	0	0	14	0	1	1	12	7	0	0	7	0	0	0	14	6	2	0	6	0	0	0	14	11	0	0	3	14
47	HIDALGO 5	2	3	1	4	0	0	0	10	8	0	0	2	4	0	0	6	2	0	0	8	8	0	0	2	0	0	0	10	10	0	0	0	10
48	13	3	0	0	5	0	0	0	8	1	2	0	5	0	0	1	7	0	0	0	8	2	0	0	6	0	0	0	8	3	1	0	4	8
49	18	6	1	0	5	5	0	2	5	7	0	0	5	2	0	1	9	3	0	0	9	12	0	0	0	0	0	0	12	12	0	0	0	12
50	22	1	2	0	7	0	0	0	10	0	1	0	9	0	1	0	9	0	0	0	10	3	3	0	4	0	0	0	10	3	0	0	7	10
51	26	8	0	0	0	0	0	0	8	0	0	0	8	0	0	0	8	0	0	0	8	0	4	0	4	0	0	0	8	0	2	0	6	8
52	33	3	4	0	5	0	0	0	12	1	0	0	11	2	0	0	10	0	0	0	12	5	0	0	7	0	0	0	12	10	1	0	1	12
53	34	0	2	0	10	0	0	0	12	0	0	0	12	5	3	0	4	0	0	0	12	5	3	0	4	0	0	0	12	12	0	0	0	12
54	37	3	0	0	7	0	0	0	10	0	0	0	10	6	0	0	4	0	0	0	10	4	1	2	3	0	0	0	10	6	0	0	4	10
55	41	3	2	0	9	0	0	0	14	0	0	0	14	0	0	0	14	0	0	0	14	0	1	0	13	0	0	0	14	1	6	0	7	14
56	46	1	2	0	3	0	0	0	6	2	0	0	4	1	0	0	5	0	0	0	6	6	0	0	0	0	0	0	6	5	0	0	1	6
57	49	0	1	0	5	0	0	0	6	0	0	0	6	1	0	0	5	0	0	0	6	4	0	0	2	0	0	0	6	5	0	0	1	6
58	MEXICO 3	0	0	0	10	0	0	0	10	0	0	1	9	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	10
59	7	0	2	1	35	0	0	1	37	0	0	1	37	0	1	0	37	0	0	0	38	0	0	2	36	0	0	0	38	0	0	2	36	38
60	7A	0	4	0	8	0	0	0	12	0	0	0	12	0	0	0	12	0	1	0	11	1	0	0	11	0	0	0	12	0	4	0	8	12
61	33	3	1	0	6	1	2	0	7	6	0	0	4	2	0	0	8	0	0	0	10	7	0	0	3	0	0	0	10	10	0	0	0	10
62	34	2	0	1	7	0	0	0	10	8	0	0	2	1	0	0	9	0	0	0	10	5	1	0	4	0	0	0	10	10	0	0	0	10
63	36	3	2	1	4	0	3	1	6	2	2	0	6	6	0	0	4	0	2	1	7	3	3	0	4	0	0	0	10	5	1	0	4	10
64	38	1	5	0	6	0	3	0	9	7	0	0	5	3	0	0	9	0	1	0	11	7	1	0	4	0	0	0	12	9	0	0	3	12
65	46	1	1	1	7	0	1	0	9	4	1	0	5	1	1	0	8	0	0	0	10	4	2	1	3	0	0	0	10	8	0	0	2	10
66	49	0	2	0	10	0	0	0	12	5	0	0	7	1	0	0	11	0	0	0	12	6	0	0	6	0	0	0	12	8	0	0	4	12
67	51	0	0	0	10	0	0	0	10	2	1	0	7	0	0	0	10	0	0	0	10	0	1	0	9	0	0	0	10	3	1	0	6	10
68	59	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	10
69	62	0	0	0	10	0	0	0	10	0	1	0	9	0	0	0	10	0	0	0	10	2	5	0	3	0	0	0	10	2	1	0	7	10
70	74	0	0	1	7	0	0	2	6	5	0	0	3	0	1	0	7	1	2	0	5	2	2	0	4	0	0	0	8	2	0	0	6	8
71	77	0	1	0	9	0	0	0	10	0	2	0	8	0	0	0	10	0	0	0	10	0	0	2	8	0	0	0	10	1	0	0	9	10
72	95	0	3	0	3	0	0	0	6	1	0	0	5	0	1	0	5	0	0	0	6	2	0	1	3	0	0	0	6	0	2	0	4	6
73	142	0	4	0	6	4	0	1	5	9	0	0	1	2	4	0	4	0	0	0	10	2	3	0	5	0	0	0	10	7	0	0	3	10
74	181	0	0	0	10	0	0	0	10	1	1	0	8	0	0	0	10	0	1	0	9	0	1	0	9	0	0	0	10	0	1	1	8	10
75	182	1	1	1	5	0	2	0	6	6	0	0	2	2	0	0	6	0	0	0	8	0	0	1	7	0	0	0	8	5	0	0	3	8
76	205	2	0	0	10	1	1	0	10	4	0	1	7	1	0	1	10	0	0	0	12	5	1	0	6	0	0	0	12	9	0	0	3	12
77	207	1	0	8	39	0	0	0	48	3	12	1	32	4	5	1	38	0	3	0	45	12	8	5	23	0	0	0	48	9	16	10	13	48
78	208	4	2	3	3	1	1	0	10	4	0	0	8	2	0	0	10	0	0	0	12	6	1	0	5	0	0	0	12	12	0	0	0	12
79	210	4	4	7	15	3	7	6	14	8	5	2	15	10	8	4	8	0	2	2	26	17	8	0	5	0	0	0	30	24	4	2	0	30
80	211	0	1	0	11	0	0	0	12	0	0	2	10	0	1	0	11	0	0	0	12	0	1	0	11	0	0	0	12	0	0	2	10	12
81	225	4	3	0	3	0	0	0	10	0	0	0	10	5	1	0	4	0	0	0	10	2	1	0	7	0	0	0	10	6	1	0	3	10
82	M-1	3	4	1	10	0	1	0	17	6	4	0	8	4	1	1	12	1	1	0	16	5	4	0	9	0	0	0	18	10	3	0	5	18
83	M-2	2	3	0	15	2	1	0	17	9	0	0	11	2	2	0	16	1	3	0	16	5	7	0	8	0	0	0	20	10	5	0	5	20
84	M-3	0	4	2	10	0	0	1	15	3	1	0	12	6	2	0	8	0	2	0	14	0	5	0	11	0	0	0	16	9	2	0	5	16
85	MICHOACAN 40	3	2	0	5	2	0	0	8	0	0	0	10	4	1	0	5	0	0	0	10	6	1	0	3	0	0	0	10	7	0	0	3	10
86	41	0	0	0	8	2	1	0	5	1	0	0	7	0	0	2	6	0	0	0	8	0	2	0	6	0	0	0	8	4	0	0	4	8
87	45	1	4	1	4	0	0	0	10	5	0	0	5	1	4	0	5	0	0	0	10	10	0	0	0	0	0	0	10	9	0	0	1	10
88	54	6	1	0	3	1	4	1	4	4	0	0	6	8	0	0	2	0	0	0	10	8	0	0	2	0	0	0	10	9	0	0	1	10

TABLE 3 (Continued).

NO. ON MAP	COLLECTION NUMBER		CHROMOSOME KNOB POSITION AND SIZE																																TOTAL NO. CHROM.
			1S2				1L1				2S1				2L1				3S1				3L1				4S2				4L1				
			l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	
89	MICHOACAN	74	8	0	0	0	0	0	0	8	3	0	0	5	7	0	0	1	0	0	0	8	3	2	0	3	0	0	0	8	7	0	0	1	8
90		78	8	1	2	3	0	0	0	14	4	0	1	9	6	1	0	7	0	1	0	13	11	0	0	3	0	0	0	14	14	0	0	0	14
91		79	10	0	0	0	1	0	0	9	1	1	0	8	7	0	0	3	2	1	0	7	8	0	0	2	0	0	0	10	7	2	0	1	10
92		105	0	4	0	6	0	0	0	10	0	0	0	10	8	0	0	2	0	1	0	9	3	1	0	6	0	0	0	10	5	4	0	1	10
93		186	0	7	0	5	0	0	1	11	0	2	0	10	7	1	0	4	0	1	0	11	9	1	0	2	0	0	0	12	9	0	0	3	12
94		191	5	5	0	2	0	0	1	11	1	1	0	10	11	0	0	1	0	1	0	11	9	0	0	3	0	0	0	12	11	0	0	1	12
95		199	4	0	0	6	2	0	0	8	1	1	1	7	4	1	0	5	1	0	0	9	5	1	0	4	0	0	0	10	9	0	0	1	10
96		200	0	6	2	4	0	0	0	12	0	0	0	12	8	2	1	1	0	0	0	12	6	4	0	2	0	0	0	12	2	8	2	0	12
97		204	0	3	1	4	1	0	0	7	6	0	0	2	5	0	1	2	1	1	0	6	5	0	0	3	0	0	0	8	3	1	0	4	8
98		211	0	6	0	4	1	2	0	7	8	0	0	2	7	0	0	3	0	0	0	10	9	0	0	1	0	0	0	10	9	0	0	1	10
99	MORELOS	1	0	7	1	2	0	0	0	10	1	0	0	9	4	1	0	5	0	0	0	10	0	2	0	8	0	0	0	10	8	0	0	2	10
100		3	0	4	0	4	0	0	0	8	4	0	0	4	1	1	0	6	0	0	0	8	5	0	0	3	0	0	0	8	8	0	0	0	8
101		13	0	4	0	2	0	0	0	6	0	0	0	6	0	1	0	5	0	0	0	6	4	0	0	2	0	0	0	6	3	2	0	1	6
102		14	7	0	0	1	0	0	0	8	0	0	0	8	3	0	0	5	0	0	0	8	0	1	0	7	0	0	0	8	8	0	0	0	8
103		15	1	1	0	4	0	0	0	6	3	0	0	3	4	2	0	0	0	0	0	6	6	0	0	0	0	0	0	6	2	3	0	1	6
104		17	0	4	0	4	0	0	0	8	1	0	0	7	6	1	0	1	0	0	0	8	2	3	0	3	0	0	0	8	6	2	0	0	8
105		18	0	1	0	5	0	0	0	6	0	0	0	6	3	0	0	3	0	0	0	6	4	0	0	2	0	0	0	6	2	1	0	3	6
106		19	10	0	0	0	0	0	0	10	3	1	3	3	3	1	0	6	0	0	0	10	3	3	0	4	0	0	0	10	8	0	0	2	10
107		22	8	1	0	3	0	0	0	12	1	0	0	11	2	1	0	9	0	0	0	12	4	0	0	8	0	0	0	12	12	0	0	0	12
108		27	0	4	0	2	0	0	0	6	1	0	0	5	2	1	0	3	0	0	0	6	4	0	0	2	0	0	0	6	5	0	0	1	6
109		60	2	2	0	4	0	0	0	8	0	2	0	6	8	0	0	0	0	0	0	8	5	1	0	2	0	0	0	8	7	0	0	1	8
110		79	3	4	0	3	0	0	0	10	0	0	0	10	5	0	0	5	0	0	0	10	6	0	0	4	0	0	0	10	7	2	0	1	10
111		93	6	0	1	3	0	0	0	10	0	0	0	10	4	0	0	6	0	0	0	10	10	0	0	0	0	0	0	10	7	0	0	3	10
112	PUEBLA	33	6	1	0	1	0	2	0	6	4	0	0	4	3	0	0	5	0	0	0	8	8	0	0	0	0	0	0	8	8	0	0	0	8
113		196	0	1	2	3	0	0	0	6	0	0	0	6	4	0	0	2	0	0	0	6	1	0	0	5	0	0	0	6	1	3	0	2	6
114		280	2	2	1	1	0	0	0	6	0	0	0	6	3	0	1	2	1	0	0	5	4	0	0	2	0	0	0	6	5	0	0	1	6
115		219	2	1	0	5	0	0	0	8	0	0	1	7	6	0	0	2	0	0	0	8	2	2	0	4	0	0	0	8	5	2	0	1	8
116		223	2	3	1	2	0	0	0	8	2	0	0	6	1	3	0	4	0	0	0	8	3	1	0	4	0	0	0	8	8	0	0	0	8
117		229	1	1	1	3	0	0	0	6	0	0	0	6	0	1	0	5	0	0	0	6	2	1	0	3	0	0	0	6	6	0	0	0	6
118	QUERETARO	1	0	5	0	5	6	0	0	4	10	0	0	0	6	0	0	4	0	0	0	10	7	0	0	3	0	0	0	10	10	0	0	0	10
119		4	0	0	0	10	0	0	0	10	7	0	0	3	5	1	0	4	1	0	0	9	6	0	0	4	0	0	0	10	9	0	0	1	10
120		15	0	0	0	6	0	0	0	6	3	0	0	3	4	0	0	2	0	0	0	6	5	0	0	1	0	0	0	6	6	0	0	0	6
121		20	3	1	1	7	5	0	0	7	8	1	0	3	6	3	0	3	1	1	0	10	10	0	0	2	0	0	0	12	5	3	1	3	12
122		29	5	1	1	3	0	0	0	10	7	0	0	3	2	1	0	7	2	0	0	8	5	2	0	3	0	0	0	10	10	0	0	0	10
123		31	4	2	0	4	2	2	0	6	3	0	2	5	4	1	0	5	0	0	0	10	4	2	0	4	0	0	0	10	10	0	0	0	10
124		34	4	0	0	2	0	0	0	6	3	0	0	3	2	0	0	4	1	0	0	5	5	0	0	1	0	0	0	6	6	0	0	0	6
125		39	4	2	1	5	0	0	0	12	2	0	6	4	8	0	0	4	0	2	0	10	2	3	0	7	0	0	0	12	12	0	0	0	12
126		43	2	4	0	6	0	0	0	12	0	1	2	9	9	0	0	3	0	0	0	12	1	1	0	10	0	0	0	12	11	0	0	1	12
127		48	0	1	0	11	0	0	0	12	0	1	0	11	6	2	0	4	0	0	0	12	0	7	0	5	0	0	0	12	7	1	0	4	12
128		49	3	3	1	3	0	1	0	9	0	0	1	9	4	1	0	5	0	0	0	10	5	0	0	5	0	0	0	10	7	0	0	3	10
129		50	1	5	0	4	0	0	0	10	0	0	0	10	8	1	0	1	0	0	0	10	4	2	0	4	0	0	0	10	5	1	1	3	10
130	S.L.POTOSI	12	0	4	1	5	0	0	0	10	0	0	1	9	0	5	2	3	0	0	0	10	0	3	0	7	0	0	0	10	0	9	0	1	10
131		78	0	2	4	6	0	0	1	11	0	0	0	12	4	6	0	2	0	0	0	12	2	4	1	5	0	0	0	10•	2	7	0	1•	12
132		95	0	0	1	5	0	0	0	6	0	0	0	6	2	4	0	0	0	0	0	6	0	0	0	6	0	0	0	6	0	6	0	0	6
133		128	0	2	3	7	0	0	0	12	0	0	0	10•	2	4	0	4•	0	0	0	12	1	5	0	6	0	0	0	10•	8	2	0	0•	12
134		150	0	0	4	8	0	0	1	11	0	0	1	11	0	12	0	0	0	0	0	12	3	5	0	4	0	0	0	12	0	11	0	1	12
135	TLAXCALA	1	1	6	0	5	1	3	0	8	4	0	0	8	1	4	0	7	0	3	0	9	9	0	0	3	0	0	0	12	5	3	0	4	12
136		3	0	1	0	11	0	0	0	12	0	6	1	5	0	2	1	9	2	2	0	8	0	5	1	6	0	0	0	12	5	3	0	4	12
137		5	4	2	0	4	5	0	0	5	5	1	0	4	1	0	0	9	5	0	0	5	4	1	0	5	0	0	0	10	8	1	0	1	10
138	VERACRUZ	215	0	1	1	8	0	0	0	10	0	0	0	10	0	7	1	2	0	0	0	10	0	4	2	4	0	0	0	10	3	4	0	3	10

TABLE 4. Frequencies for the different knob sizes of the 5S1, 5L1, 6L1, 6L2, 6L3, 7S, 7L1, and 8L1 knob positions found in each of the maize collections examined from regions of central Mexico. The first column, number on map, refers to the numbering of the collections in the collection distribution map given in the text. The small letters l, m, s, and o, indicate large, medium, and small knob sizes and the knobless condition respectively. Knob frequencies marked with an asterisk indicate that the total number of chromosomes examined was less than the one given in the rightmost column.

NO. ON MAP	COLLECTION NUMBER		CHROMOSOME KNOB POSITION AND SIZE																														TOTAL NO. CHROM.
			5S1				5L1				6L1				6L2				6L3				7S				7L1				8L1				
			l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	
1	GUANAJUATO	2	0	0	0	10	8	0	0	2	0	1	0	9	0	0	4	6	0	2	2	6	0	0	0	10	8	2	0	0	5	2	0	3	10
2		3	0	0	0	12	12	0	0	0	0	2	4	6	0	0	6	6	0	0	5	7	0	0	0	12	10	0	0	2	12	0	0	0	12
3		10	0	0	0	12	11	0	0	1	0	2	0	10	0	0	7	5	0	2	5	5	0	0	0	12	9	1	0	2	12	0	0	0	12
4		16	0	0	0	6	6	0	0	0	0	3	0	3	0	0	3	3	4	1	0	1	0	0	0	6	6	0	0	0	5	0	0	1	6
5		21	0	0	0	8	6	0	0	2	0	2	0	6	0	0	0	8	3	0	0	5	0	0	0	8	4	0	0	4	2	4	0	2	8
6		24	0	0	0	10	5	1	1	3	0	1	3	6	0	0	2	8	0	2	3	5	0	0	0	10	9	1	0	0	4	1	0	5	10
7		28	0	0	0	10	8	0	0	2	0	2	2	6	0	0	2	8	0	5	2	3	0	0	0	10	8	0	0	2	6	1	0	3	10
8		30	0	0	0	8	7	0	0	1	4	0	0	4	0	0	3	5	0	4	0	4	0	0	0	8	5	0	0	3	4	0	0	4	8
9		36	0	0	0	12	10	0	0	2	0	1	0	11	0	0	4	8	0	3	3	6	0	0	0	12	4	4	0	4	2	5	0	5	12
10		42	0	0	0	12	12	0	0	0	0	4	0	8	0	0	0	12	0	0	5	7	0	0	0	12	7	1	0	4	8	1	0	3	12
11		51	0	0	0	10	7	0	0	3	0	0	0	10	0	0	6	4	0	6	1	3	0	0	0	10	9	0	0	1	10	0	0	0	10
12		69	0	0	0	10	5	1	1	3	0	0	0	10	0	0	3	7	2	0	2	6	0	0	0	10	7	0	0	3	8	0	0	2	10
13		71	0	0	0	12	8	0	0	4	2	2	0	8	0	0	3	9	1	0	7	4	0	0	0	12	10	0	0	2	7	1	0	4	12
14		91	0	0	0	10	9	1	0	0	0	0	1	9	0	0	4	6	0	1	2	7	0	0	0	10	5	3	0	2	5	3	0	2	10
15		100	0	0	0	12	12	0	0	0	0	0	0	12	0	0	7	5	0	0	6	6	0	0	0	12	12	0	0	0	10	0	0	2	12
16		101	0	0	0	32	13	16	1	2	0	0	6	26	0	0	19	13	0	6	12	14	0	0	0	32	12	11	6	3	18	11	0	3	32
17		102	0	0	0	10	10	0	0	0	0	0	0	10	0	0	3	7	0	0	4	6	0	0	0	10	10	0	0	0	4	5	0	1	10
18	GUERRERO	3	0	0	0	6	5	0	0	1	0	0	0	6	0	0	0	6	0	2	0	4	0	0	0	6	2	1	1	2	5	0	0	1	6
19		4	0	0	0	8	8	0	0	0	0	0	0	8	0	0	1	7	0	2	1	5	0	0	0	8	2	1	1	4	1	0	0	7	8
20		6	0	0	0	10	10	0	0	0	0	0	0	8*	0	0	2	6*	0	0	4	4*	0	0	0	10	5	1	0	4	1	3	1	5	10
21		8	2	0	0	2	1	0	1	2	0	0	0	4	0	0	1	3	0	1	1	2	0	0	0	4	2	0	1	1	1	2	0	1	4
22		9	0	0	0	6	4	0	0	2	0	0	0	6	0	0	3	3	2	0	2	2	0	0	0	6	6	0	0	0	4	1	0	1	6
23		36	0	0	0	12	3	5	2	2	0	1	0	11	0	0	4	8	0	0	5	7	0	0	0	12	2	5	2	3	4	4	1	3	12
24		39	0	0	0	10	9	0	0	1	0	0	0	10	0	0	1	9	0	0	2	8	0	0	0	10	8	1	0	1	0	1	1	8	10
25		60	0	0	0	12	11	0	0	1	0	0	0	12	0	2	2	8	0	0	5	7	0	0	0	12	5	3	0	4	3	5	0	4	12
26		77	1	0	0	5	4	0	0	2	0	0	0	6	0	0	2	4	0	0	3	3	0	0	0	6	4	1	0	1	2	1	0	3	6
27		96	0	0	0	10	6	2	0	2	0	0	0	10	0	0	9	1	0	0	4	6	0	0	0	10	4	5	0	1	10	0	0	0	10
28		99	0	0	0	6	6	0	0	0	0	0	0	6	0	1	4	1	0	2	2	2	0	0	0	6	6	0	0	0	4	1	0	1	6
29		106	0	1	0	9	7	2	0	1	0	0	0	10	0	0	3	7	0	1	5	4	0	2	0	8	7	1	0	2	2	4	0	4	10
30		134	0	0	0	10	0	9	0	1	0	0	0	10	0	1	6	3	0	1	6	3	0	2	0	8	0	10	0	0	0	6	0	4	10
31		150	0	0	0	12	0	10	2	0	0	0	0	12	0	0	8	4	0	0	7	5	0	0	0	12	6	3	3	0	0	9	0	3	12
32		153	0	0	0	12	4	4	2	2	0	0	1	11	0	0	8	4	0	0	7	5	0	2	0	10	1	8	0	3	0	10	2	0	12
33		166	0	0	0	6	3	3	0	0	0	0	0	6	0	1	3	2	0	1	2	3	0	0	0	6	0	6	0	0	0	5	0	1	6
34		200	0	0	0	12	9	2	0	1	0	0	0	12	0	0	8	4	0	0	5	7	0	0	0	12	7	5	0	0	4	5	0	3	12
35		208	0	0	0	10	8	2	0	0	0	0	0	10	0	0	7	3	0	0	5	5	0	0	0	10	8	0	0	2	5	3	0	2	10
36		210	0	0	0	8	2	5	0	1	0	0	0	8	0	0	6	2	0	0	5	3	0	0	1	7	0	6	2	0	1	3	2	2	8
37		212	0	0	0	12	2	8	1	1	0	0	0	12	0	0	7	5	0	0	5	7	0	2	0	10	7	4	0	1	0	3	3	6	12
38		217	0	0	0	10	7	1	0	2	0	0	0	10	0	0	4	6	0	0	6	4	0	1	0	9	9	0	0	1	1	3	0	6	10

TABLE 4 (Continued).

NO. ON MAP.	COLLECTION NUMBER		CHROMOSOME KNOB POSITION, AND SIZE																																				TOTAL NUM. CHROM.
			5S1				5L1				6L1				6L2				6L3				7S				7L1				8L1				
			l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	O	l	m	s	o	l	m	s	o	l	m	s	o	
39	GUERRERO	221	0	0	0	18	8	1	8	1	0	0	0	18	0	0	6	12	0	6	3	9	1	0	0	17	12	0	2	4	5	6	0	7	18
40		222	0	0	0	12	10	0	0	2	0	0	0	12	0	0	5	7	1	3	1	7	0	0	0	12	11	1	0	0	5	1	0	6	12
41		225	0	0	0	10	9	1	0	0	0	0	0	10	0	0	1	9	1	1	1	7	0	2	0	8	10	0	0	0	7	0	0	3	10
42		228	0	0	0	10	10	0	0	0	0	0	0	10	0	0	1	9	1	2	1	6	0	1	0	9	7	1	0	2	5	2	0	3	10
43		Beadle 1a	0	0	0	34	33	0	0	1	0	0	1	33	0	1	11	22	0	14	5	15	0	0	0	34	18	2	2	12	5	7	0	22	34
44		Beadle 1b	0	0	0	42	33	1	0	8	0	0	0	42	0	0	16	26	1	11	7	23	0	0	0	42	12	10	2	18	4	10	0	28	42
45		Beadle 2	0	0	0	34	27	2	0	5	0	0	0	34	0	0	1	33	0	1	8	25	0	0	0	34	13	10	0	11	3	7	0	24	34
46		Beadle 3	0	0	0	14	9	1	0	4	0	0	1	13	0	1	0	13	0	2	3	9	1	0	0	13	8	2	0	4	2	0	1	11	14
47	HIDALGO	5	0	0	0	10	7	0	0	3	2	5	0	3	0	0	0	10	0	0	0	10	0	0	0	10	9	0	0	1	8	0	0	2	10
48		13	0	0	0	8	4	1	0	3	0	0	0	8	0	0	0	8	0	0	3	5	0	0	0	8	2	1	0	5	0	1	0	7	8
49		18	0	0	0	12	12	0	0	0	0	8	0	4	0	0	1	11	0	2	1	9	0	0	0	12	8	0	0	4	4	4	0	4	12
50		22	0	0	0	10	8	0	0	2	0	4	0	6	0	0	0	10	0	1	2	7	0	0	0	10	0	5	0	5	4	0	0	6	10
51		26	0	0	0	8	4	0	0	4	0	0	0	8	0	0	0	8	0	0	0	8	0	0	0	8	0	0	0	8	0	0	0	8	8
52		33	0	0	0	12	10	0	0	2	0	0	0	12	0	0	6	6	0	3	5	4	0	0	0	12	12	0	0	0	6	4	0	2	12
53		34	0	0	0	12	9	2	0	1	0	0	0	12	0	0	5	7	0	2	3	7	0	0	0	12	6	4	0	2	4	4	0	4	12
54		37	0	0	0	10	10	0	0	0	0	0	1	9	0	0	4	6	0	1	3	6	0	0	0	10	7	0	0	3	9	0	1	0	10
55		41	0	0	0	14	0	6	2	6	0	0	0	14	0	0	2	12	0	3	2	9	0	0	0	14	10	4	0	0	7	3	0	4	14
56		45	0	0	0	6	5	0	0	1	0	0	0	6	0	0	1	5	1	2	2	1	0	0	0	6	5	0	0	1	0	2	0	4	6
57		49	0	0	0	6	3	0	0	3	0	0	0	6	0	0	4	2	0	0	1	5	0	0	0	6	3	0	1	2	3	0	0	3	6
58	MEXICO	3	0	0	0	10	0	3	2	5	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	0	2	0	8	0	0	0	10	10
59		7	0	0	0	38	4	1	17	16	0	0	1	37	0	0	0	38	0	0	0	38	0	0	0	38	0	0	1	37	0	0	2	36	38
60		71	0	0	0	12	0	6	0	6	0	2	0	10	0	0	0	12	0	0	0	12	0	0	0	12	0	0	0	12	0	0	0	12	12
61		33	0	0	0	10	10	0	0	0	0	0	2	8	0	0	0	10	0	0	4	6	0	0	0	10	7	0	0	3	5	3	0	2	10
62		34	0	0	0	10	10	0	0	0	0	0	1	9	0	0	0	10	0	0	0	10	0	0	0	10	6	1	0	3	0	7	0	3	10
63		36	0	0	0	10	6	0	0	4	0	4	0	6	0	0	1	9	0	0	2	8	0	0	0	10	2	4	0	4	1	5	0	4	10
64		38	0	0	0	12	10	0	0	2	0	2	2	8	0	0	0	12	0	0	2	10	0	0	0	12	9	0	0	3	3	6	0	3	12
65		46	0	0	0	10	5	0	0	5	0	5	0	5	0	0	0	10	0	0	3	7	0	0	0	10	7	0	0	3	4	2	0	4	10
66		49	0	0	0	12	9	0	0	3	0	2	0	10	0	0	0	12	0	0	0	12	0	0	0	12	5	1	0	6	0	0	0	12	12
67		51	0	0	0	10	5	0	0	5	0	2	0	8	0	0	0	10	0	0	2	8	0	0	0	10	4	2	0	4	0	2	0	8	10
68		59	0	0	0	10	1	3	0	6	0	2	0	8	0	0	0	10	0	0	2	8	0	0	0	10	1	1	0	8	0	0	0	10	10
69		62	0	0	0	10	2	1	2	5	0	2	1	7	0	0	0	10	0	1	1	8	0	0	0	10	6	0	0	4	0	6	0	4	10
70		74	0	0	0	8	5	0	0	3	0	2	2	4	0	0	0	8	0	0	2	6	0	0	0	8	3	1	0	4	0	1	2	5	8
71		77	0	0	0	10	2	2	1	5	0	1	0	9	0	0	0	10	0	0	2	8	0	0	0	10	2	0	0	8	0	2	0	8	10
72		95	0	0	0	6	1	2	0	3	0	0	0	6	0	0	0	6	0	2	0	4	0	0	0	6	2	0	1	3	2	0	0	4	6
73		142	0	0	0	10	5	1	0	4	0	5	0	5	0	0	2	8	0	0	0	10	0	0	4	6	6	0	0	4	3	2	0	5	10
74		181	0	0	0	10	4	2	0	4	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	0	1	2	7	0	1	1	8	10
75		182	0	0	0	8	5	0	0	3	0	0	0	8	0	0	0	8	0	0	0	8	0	1	0	7	6	0	0	2	0	0	3	5	8
76		205	0	0	0	12	8	0	0	4	0	1	0	11	0	0	0	12	0	2	1	9	0	0	0	12	5	1	0	6	2	2	0	8	12
77		207	0	0	0	48	4	18	16	10	0	3	2	43	0	0	0	48	0	0	10	38	0	0	0	48	2	6	13	27	2	6	2	38	48
78		208	0	0	0	12	11	0	0	1	0	2	0	10	0	0	0	12	0	0	1	11	0	0	0	12	10	0	0	2	0	4	0	8	12
79		210	2	0	0	28	24	6	0	0	1	3	6	20	0	1	4	25	0	12	7	11	0	0	0	30	16	8	2	4	2	7	5	16	30
80		211	0	0	0	12	4	4	0	4	0	0	0	12	0	0	0	12	0	0	2	10	0	0	0	12	0	2	1	9	0	0	0	12	12
81		225	0	0	0	10	10	0	0	0	0	0	0	10	0	1	1	8	1	0	3	6	0	0	0	10	6	0	0	4	1	1	1	7	10
82		M-1	0	0	0	18	12	1	0	5	0	7	0	11	0	0	0	18	0	0	2	16	0	0	0	18	9	2	1	6	1	7	0	10	18
83		M-2	0	0	0	20	13	3	0	4	0	10	0	10	0	0	2	18	0	0	2	18	0	0	0	20	14	0	0	6	2	6	1	11	20
84		M-3	0	0	0	16	12	1	0	3	0	2	2	2	0	0	2	14	0	0	1	15	0	0	0	16	8	2	0	6	2	3	2	9	16
85	MICHOACAN	40	0	0	0	10	9	0	0	1	0	0	0	10	0	0	4	6	0	2	3	5	0	0	0	10	9	0	0	1	4	0	0	6	10
86		41	0	0	0	8	6	0	0	2	0	0	0	8	0	0	0	8	1	0	2	5	0	0	0	8	0	0	1	7	0	0	0	8	8
87		45	0	0	0	10	10	0	0	0	0	0	3	7	0	0	0	10	0	0	0	10	0	1	0	9	7	1	0	2	1	7	0	2	10
88		54	0	0	0	10	8	0	0	2	0	1	1	8	0	0	6	4	0	0	2	8	0	0	0	10	8	0	0	2	7	1	0	2	10

TABLE 4 (Continued).

NO. ON MAP	COLLECTION NUMBER		CHROMOSOME KNOB POSITION AND SIZE																																TOTAL NO. CHROM.
			5S1				5L1				6L1				6L2				6L3				7S				7L1				8L1				
			l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	
89	MICHOACAN	74	0	0	0	8	5	1	0	2	0	0	0	8	0	1	2	5	5	0	1	2	0	4	0	4	8	0	0	0	5	0	0	3	8
90		78	2	0	0	12	11	1	0	2	0	3	0	11	0	0	3	11	0	2	5	7	0	0	0	14	10	2	0	2	9	4	0	1	14
91		79	0	0	0	10	9	0	0	1	0	2	0	8	0	0	3	7	0	1	1	8	0	0	0	10	5	2	0	3	9	0	0	1	10
92		105	0	0	0	10	1	7	1	1	0	0	0	10	0	0	6	4	0	1	5	4	0	2	2	6	0	8	0	2	3	2	1	4	10
93		186	0	0	0	12	7	1	1	3	1	1	0	10	0	0	3	9	0	2	5	5	0	0	0	12	8	1	0	3	3	5	0	4	12
94		191	0	2	0	10	10	0	0	2	0	0	0	12	0	0	2	10	0	3	4	5	0	0	1	11	3	5	0	4	5	2	0	5	12
95		199	0	0	0	10	6	0	1	3	1	1	1	7	0	0	2	8	0	0	3	7	0	1	0	9	7	0	1	2	2	2	0	6	10
96		200	0	0	0	12	6	6	0	0	0	0	0	12	0	0	6	6	0	0	6	6	0	0	0	12	1	9	0	2	4	7	0	1	12
97		204	0	0	0	8	8	0	0	0	1	2	1	4	0	0	1	7	0	0	3	5	0	0	0	8	6	0	0	2	0	3	1	4	8
98		211	0	0	0	10	8	0	0	2	0	0	5	5	0	0	1	9	2	0	0	8	0	0	0	10	6	1	1	2	2	4	0	4	10
99	MORELOS	1	0	0	0	10	8	0	1	1	0	0	0	10	0	0	2	8	0	0	4	6	0	0	0	10	10	0	0	0	1	2	3	4	10
100		3	0	0	0	8	6	0	1	1	0	0	0	8	0	0	0	8	1	2	0	5	0	0	0	8	5	1	0	2	3	0	0	5	8
101		13	0	0	0	6	5	0	0	1	0	0	0	6	0	0	0	6	1	0	0	5	0	0	0	6	0	3	0	3	5	0	0	1	6
102		14	0	0	0	8	6	0	1	1	0	0	0	8	0	0	1	7	0	2	1	5	0	0	0	8	4	2	0	2	1	1	1	5	8
103		15	0	0	0	6	5	0	0	1	0	0	0	6	0	0	1	5	1	1	0	4	0	0	0	6	5	0	0	1	6	0	0	0	6
104		17	0	0	1	7	6	0	1	1	0	0	0	8	0	0	4	4	0	3	1	4	0	0	0	8	5	2	0	1	1	2	0	5	8
105		18	0	0	0	6	6	0	0	0	0	0	0	6	0	0	1	5	1	0	2	3	0	1	0	5	4	0	0	2	3	1	0	2	6
106		19	0	0	0	10	10	0	0	0	0	0	0	10	0	0	4	6	2	0	4	4	0	0	0	10	9	0	0	1	5	0	0	5	10
107		22	0	0	0	12	11	0	0	1	0	0	0	12	0	0	6	6	0	3	1	8	0	0	0	12	9	0	0	3	1	1	1	9	12
108		27	0	0	0	6	5	0	0	1	0	1	0	5	0	0	2	4	0	2	0	4	0	1	0	5	4	0	0	2	6	0	0	0	6
109		60	0	0	0	8	3	3	0	2	0	1	0	7	0	0	1	7	0	4	0	4	0	0	0	8	8	0	0	0	4	2	0	2	8
110		79	0	0	0	10	10	0	0	0	0	0	0	10	0	0	0	10	1	1	2	6	0	0	0	10	9	0	0	1	6	1	0	3	10
111		93	0	0	0	10	8	0	0	2	0	0	0	10	0	0	2	8	1	2	1	6	0	1	0	9	9	0	0	1	5	1	0	4	10
112	PUEBLA	33	0	0	0	8	8	0	0	0	3	0	0	5	0	0	0	8	0	1	2	5	0	0	0	8	7	0	0	1	3	0	0	5	8
113		196	0	0	0	6	6	0	0	0	0	0	0	6	0	0	1	5	2	0	1	3	0	0	1	5	4	1	0	1	6	0	0	0	6
114		200	2	0	0	4	4	1	0	1	0	0	0	6	0	0	0	6	2	2	1	1	0	1	0	5	4	0	0	2	4	1	0	1	6
115		219	0	0	0	8	8	0	0	0	0	0	0	8	0	0	4	4	0	1	1	6	0	0	0	8	8	0	0	0	2	2	0	4	8
116		223	0	0	0	8	7	0	0	1	0	0	0	8	0	0	0	8	0	1	1	6	0	0	1	7	6	0	0	2	3	3	0	2	8
117		229	0	0	0	4•	3	0	0	1•	0	0	0	6	0	0	0	6	0	0	2	4	0	0	0	6	4	0	0	2	2	0	1	1•	6
118	QUERETARO	1	0	0	0	10	9	0	0	1	0	6	0	4	0	0	0	10	0	1	0	9	0	0	0	10	8	0	0	2	3	4	0	3	10
119		4	0	0	0	10	9	0	0	1	0	0	1	9	0	0	0	10	0	2	2	6	0	0	0	10	9	0	0	1	3	1	0	6	10
120		15	0	0	0	6	6	0	0	0	0	0	0	6	0	0	5	1	0	0	4	2	0	0	0	6	6	0	0	0	6	0	0	0	6
121		20	0	0	0	12	11	0	0	1	0	5	1	6	0	0	0	12	0	1	2	9	0	0	0	12	5	4	0	3	3	6	0	3	12
122		29	0	0	0	10	10	0	0	0	0	5	0	5	0	0	3	7	0	3	2	5	0	0	0	10	9	1	0	0	4	4	0	2	10
123		31	0	0	0	10	10	0	0	0	0	2	1	7	0	0	4	6	0	0	3	7	0	0	0	10	7	0	0	3	4	3	0	3	10
124		34	0	0	0	6	6	0	0	0	1	2	0	3	0	0	1	5	0	1	1	4	0	0	0	6	4	0	0	2	6	0	0	0	6
125		39	0	0	0	12	12	0	0	0	0	0	0	12	0	0	2	10	0	3	3	6	0	0	0	12	12	0	0	0	10	1	0	1	12
126		43	0	0	0	12	11	0	0	1	0	0	0	12	0	0	3	9	0	5	4	3	0	0	0	12	8	0	0	4	10	0	0	2	12
127		48	0	0	0	12	3	4	1	4	0	0	0	12	0	0	1	11	0	1	4	7	0	0	0	12	2	8	0	2	1	7	0	4	12
128		49	0	0	0	10	8	1	0	1	0	0	0	10	0	0	5	5	0	1	4	5	0	0	0	10	4	4	1	1	4	0	0	6	10
129		50	0	0	0	10	3	3	0	4	0	0	0	10	0	0	6	4	0	4	3	3	0	0	0	10	3	6	0	1	5	1	0	4	10
130	S.L.POTOSI	12	0	0	0	10	2	7	0	1	0	3	0	7	0	0	3	7	0	0	4	6	0	4	0	6	0	9	0	1	5	4	0	1	10
131		78	0	0	0	12	2	9	0	1	0	0	0	12	0	0	7	5	0	0	7	5	0	0	0	12	10	2	0	0	2	5	1	4	12
132		95	0	0	0	6	0	4	1	1	0	0	0	6	0	0	1	5	0	0	3	3	0	0	0	6	2	4	0	0	0	4	0	2	6
133		128	0	0	0	10•	8	2	0	0•	0	0	0	12	0	0	6	6	0	0	7	5	0	0	0	12	2	9	0	1	2	9	0	1	12
134		150	0	0	0	12	0	10	1	1	0	0	2	10	0	0	8	4	0	0	9	3	0	0	0	12	0	9	0	3	4	6	1	1	12
135	TLAXCALA	1	0	0	0	12	6	3	0	3	0	4	0	8	0	0	0	12	0	0	4	8	0	0	0	12	4	5	0	3	0	8	0	4	12
136		3	0	0	0	12	10	0	0	2	0	0	3	9	0	0	0	12	0	0	1	11	0	0	0	12	4	0	1	7	1	7	0	4	12
137		5	0	0	0	10	7	0	0	3	0	2	0	8	0	0	0	10	0	1	1	8	0	0	0	10	7	0	0	3	3	3	0	4	10
138	VERACRUZ	215	0	0	0	10	2	7	1	0	0	0	0	10	0	0	5	5	0	2	5	3	0	0	0	10	4	6	0	0	0	8	1	1	10

TABLE 5. Frequencies for the different knob sizes of the 8L2, 9S, 9L2, 10L1 and 10L2 knob positions and of the type I and II of the abnormal chromosome 10 (10 ab) and B chromosomes found in each of the maize collections examined from regions of central Mexico. The first column, number on map, refers to the numbering of the collections in the collection distribution map given in the text. The small letters l, m, s, and o, indicate large, medium, and small knob sizes and the knobless condition respectively. Knob frequencies marked with an asterisk indicate that the total number of chromosomes examined was less than the one given in the rightmost column.

NO. ON MAP	COLLECTION NUMBER		CHROMOSOME KNOB POSITION AND SIZE																							B CHROMOSOME				TOTAL NUM. CHROM.
			8L2				9S				9L2				10L1				10L2				10 ab			PLANTS		TOTAL B's	TOTAL PLANTS	
			l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	1	2	0	WITH	WITH-OUT			
1	GUANAJUATO	2	0	0	0	10	7	0	0	3	0	0	0	10	0	0	0	10	0	1	1	8	0	0	10	4	1	9	5	10
2		3	0	0	0	12	7	0	0	5	0	0	0	12	0	0	0	12	0	0	1	11	0	0	12	0	6	0	6	12
3		10	0	0	1	11	5	0	1	6	3	0	0	9	0	0	0	12	0	0	3	9	0	0	12	0	6	0	6	12
4		16	0	0	2	4	4	0	0	2	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	0	3	0	3	6
5		21	0	0	0	8	5	0	0	3	0	0	0	8	0	0	0	8	0	0	1	7	0	0	8	4	0	14	4	8
6		24	0	0	2	8	3	2	0	5	0	0	0	10	0	0	0	10	0	0	2	8	0	0	10	2	3	4	5	10
7		28	0	0	2	8	3	0	1	6	0	1	0	9	0	0	0	10	0	0	0	10	1	0	9	0	5	0	5	10
8		30	0	0	0	8	3	1	0	4	0	3	0	5	0	0	0	8	0	0	1	7	0	0	8	3	1	4	4	8
9		36	0	0	0	12	7	1	0	4	0	6	0	6	0	0	0	12	0	0	3	9	0	0	12	2	4	3	6	12
10		42	0	0	0	12	8	0	0	4	0	0	0	12	0	0	0	12	0	0	1	11	0	0	12	2	4	2	6	12
11		51	0	0	2	8	3	1	3	3	0	0	0	10	0	0	0	10	0	0	2	8	0	0	10	0	5	0	5	10
12		69	0	0	3	7	4	2	0	4	1	2	0	7	0	0	0	10	0	0	0	10	0	0	10	3	2	6	5	10
13		71	0	0	0	12	9	0	0	3	0	0	0	12	0	0	0	12	0	0	0	12	0	0	12	0	6	0	6	12
14		91	0	0	0	10	2	2	1	5	0	0	0	10	0	0	0	10	0	2	0	8	0	0	10	0	5	0	5	10
15		100	0	0	0	12	7	0	2	3	0	0	0	12	0	0	0	12	0	0	3	9	0	0	12	0	6	0	6	12
16		101	0	0	8	24	11	1	11	9	0	14	6	12	0	0	0	32	0	0	12	20	3	0	29	3	13	6	16	32
17		102	0	0	0	10	6	0	1	3	0	1	0	9	0	0	0	10	0	0	2	8	0	0	10	2	3	5	5	10
18	GUERRERO	3	0	0	3	3	3	2	0	1	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	3	0	3	3	6
19		4	0	0	0	8	0	4	0	4	0	0	1	7	0	0	0	8	0	0	0	8	0	0	8	3	1	3	4	8
20		6	0	0	1	9	8	1	0	1	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
21		8	0	0	0	4	1	2	0	1	0	1	0	3	0	0	0	4	0	0	0	4	0	0	4	1	1	1	2	4
22		9	0	0	2	4	2	2	0	2	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	0	3	0	3	6
23		36	0	0	2	10	1	0	1	10	1	3	2	6	0	0	0	12	0	0	2	10	0	0	12	4	2	6	6	12
24		39	0	0	6	4	1	6	1	2	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
25		60	0	0	5	7	3	0	2	7	1	1	0	10	0	0	0	12	0	0	0	12	0	0	12	0	6	0	6	12
26		77	0	0	0	6	0	2	2	2	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	1	2	1	3	6
27		96	0	0	9	1	2	2	3	3	0	1	1	8	0	0	0	10	0	0	0	10	4	0	6	0	5	0	5	10
28		99	0	0	5	1	6	0	0	0	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	0	3	0	3	6
29		106	0	0	5	5	8	1	0	1	0	0	2	8	0	0	0	10	0	0	0	10	3	0	7	0	5	0	5	10
30		134	0	0	5	5	0	2	0	8	0	0	2	8	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
31		150	0	0	4	8	0	3	1	8	0	0	3	9	0	0	0	12	0	0	0	12	0	0	12	0	6	0	6	12
32		153	0	0	7	5	0	2	2	8	2	2	1	7	0	0	0	12	0	0	0	12	0	0	12	0	6	0	6	12
33		166	0	0	4	2	0	0	0	6	0	0	0	6	0	0	0	6	0	0	2	4	0	0	6	0	3	0	3	6
34		200	0	0	5	7	7	2	0	3	0	4	1	7	0	0	0	12	0	0	0	12	0	0	12	0	6	0	6	12
35		208	0	0	3	7	4	3	0	3	1	2	0	7	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
36		210	0	0	6	2	1	2	0	5	0	4	1	3	0	0	0	8	0	0	0	8	1	0	7	0	4	0	4	8
37		212	0	0	8	4	0	4	2	6	0	7	0	5	0	0	0	12	0	0	1	11	0	0	12	1	5	1	6	12
38		217	0	0	6	4	2	4	0	4	0	1	1	8	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10

TABLE 5 (Continued).

NO. ON MAP	COLLECTION NUMBER	CHROMOSOME KNOB POSITION AND SIZE																							B CHROMOSOME				TOTAL NUM. CHROM.
		8L2				9S				9L2				10L1				10L2				10ab			PLANTS		TOTAL B's	TOTAL PLANTS	
		l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	1	2	0	WITH	WITH-OUT			
39	GUERRERO 221	0	0	6	12	8	0	4	6	0	0	0	18	0	0	0	18	0	0	0	18	0	0	18	1	8	2	9	18
40	222	0	0	1	11	7	1	1	3	0	0	0	12	0	0	0	12	0	0	0	12	0	0	12	1	5	2	6	12
41	225	0	0	4	6	5	1	0	4	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	3	2	5	5	10
42	228	0	0	0	10	7	1	0	2	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
43	Beadle 1a	0	0	5	29	25	1	0	8	0	0	0	34	0	0	0	34	0	0	0	34	0	0	34	1	16	2	17	34
44	Beadle 1b	0	0	5	37	26	7	0	9	0	0	0	42	0	0	0	42	0	0	0	42	0	0	42	1	20	2	21	42
45	Beadle 2	0	0	2	32	26	0	2	6	0	0	0	34	0	0	0	34	0	0	2	32	0	0	34	1	16	2	17	34
46	Beadle 3	0	0	2	12	8	1	2	3	0	0	0	14	0	0	0	14	0	0	0	14	1	0	13	2	5	2	7	14
47	HIDALGO 5	0	0	0	10	8	1	0	1	0	0	0	10	0	0	0	10	0	0	2	8	0	0	10	0	5	0	5	10
48	13	0	0	0	8	0	0	1	7	0	0	0	8	0	0	0	8	0	0	0	8	0	0	8	0	4	0	4	8
49	18	0	0	0	12	11	0	0	1	0	0	0	12	0	0	0	12	0	0	3	9	2	0	10	0	6	0	6	12
50	22	0	0	1	9	3	0	0	7	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
51	26	0	0	0	8	0	0	0	8	0	0	0	8	0	0	0	8	0	0	0	8	0	0	8	0	4	0	4	8
52	33	0	0	2	10	0	4	1	7	1	1	1	9	0	1	0	11	0	0	0	12	0	0	12	0	6	0	6	12
53	34	0	0	1	11	3	3	0	6	2	5	0	5	0	0	0	12	0	0	0	12	0	0	12	3	3	3	6	12
54	37	0	0	2	8	2	0	1	7	2	0	0	8	0	0	0	10	0	0	0	10	2	0	8	2	3	8	5	10
55	41	0	0	2	12	0	0	0	14	0	0	0	14	0	0	0	14	0	0	0	14	0	0	14	0	7	0	7	14
56	46	0	0	0	6	0	0	0	6	1	0	1	4	0	0	0	6	0	0	0	6	0	0	6	0	3	0	3	6
57	49	0	0	2	4	0	0	0	6	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	0	3	0	3	6
58	MEXICO 3	0	0	0	10	0	1	0	9	0	0	0	10	0	0	0	10	0	0	1	9	0	0	10	0	5	0	5	10
59	7	0	0	1	37	0	0	3	35	0	0	0	38	0	0	0	38	0	0	0	38	0	0	38	0	19	0	19	38
60	7A	0	0	0	12	0	0	0	12	0	0	0	12	0	0	0	12	0	0	0	12	0	0	12	0	6	0	6	12
61	33	0	0	0	10	5	0	0	5	0	0	0	10	0	0	0	10	0	0	0	10	4	0	6	0	5	0	5	10
62	34	0	0	0	10	2	2	0	6	0	0	0	10	0	0	0	10	0	0	2	8	4	0	6	0	5	0	5	10
63	36	0	0	0	10	5	0	0	5	0	0	0	10	0	0	0	10	0	0	2	8	0	0	10	0	5	0	5	10
64	38	0	0	0	12	8	0	0	4	0	0	0	12	0	0	0	12	0	0	3	9	0	0	12	0	6	0	6	12
65	46	0	0	0	10	3	2	0	5	0	0	0	10	0	0	0	10	0	0	2	8	1	0	9	0	5	0	5	10
66	49	0	0	0	12	8	0	0	4	0	0	0	12	0	0	0	12	0	0	0	12	3	0	9	0	6	0	6	12
67	51	0	0	0	10	1	2	0	7	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
68	59	0	0	0	10	0	2	1	7	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
69	62	0	0	0	10	4	1	0	5	0	0	0	10	0	0	0	10	0	0	2	8	0	0	10	1	4	1	5	10
70	74	0	0	0	8	1	2	0	5	0	0	0	8	0	0	0	8	0	0	0	8	0	0	8	0	4	0	4	8
71	77	0	0	0	10	2	0	0	8	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	2	3	5	5	10
72	95	0	0	0	6	1	2	0	3	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	2	1	4	3	6
73	142	0	0	0	10	7	0	0	3	0	0	0	10	0	0	0	10	0	0	4	6	0	0	10	0	5	0	5	10
74	181	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
75	182	0	0	0	8	5	0	0	3	0	0	0	8	0	0	0	8	0	0	2	6	0	0	8	0	4	0	4	8
76	205	0	0	0	12	4	0	0	8	0	0	0	12	0	0	0	12	0	0	0	12	1	0	11	1	5	2	6	12
77	207	0	0	0	48	2	6	6	34	0	0	0	48	0	0	0	48	0	0	4	44	0	0	48	1	23	1	24	48
78	208	0	0	0	12	7	0	2	3	0	0	0	12	0	0	0	12	0	0	1	11	0	0	12	1	5	2	6	12
79	210	0	0	0	30	18	4	1	7	0	0	1	29	0	0	0	30	0	0	7	23	0	0	30	4	11	8	15	30
80	211	0	0	1	11	0	0	0	12	0	0	0	12	0	0	0	12	0	0	1	11	0	0	12	0	6	0	6	12
81	225	0	0	2	8	6	2	0	2	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
82	M-1	0	0	0	18	6	3	1	8	0	0	0	18	0	0	0	18	0	0	0	18	1	0	17	0	9	0	9	18
83	M-2	0	0	1	19	10	3	0	7	0	0	0	20	0	0	0	20	0	0	1	19	0	0	20	0	10	0	10	20
84	M-3	0	0	0	16	11	0	0	5	0	0	0	16	0	0	0	16	0	0	1	15	1	0	15	1	7	1	8	16
85	MICHOACAN 40	0	0	0	10	2	1	0	7	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	2	3	3	5	10
86	41	0	0	0	8	0	0	0	8	0	0	0	8	0	0	0	8	0	0	1	7	0	0	8	2	2	4	4	8
87	45	0	0	0	10	8	0	0	2	0	0	0	10	0	0	0	10	0	0	0	10	4	0	6	0	5	0	5	10
88	54	0	0	3	7	9	0	0	1	1	0	0	9	0	0	0	10	0	0	0	10	3	0	7	0	5	0	5	10

TABLE 5 (Continued).

NO. ON MAP	COLLECTION NUMBER		CHROMOSOME KNOB POSITION AND SIZE																					B CHROMOSOME				TOTAL NUM. CHROM.
			8L2				9S				9L2				10L1				10L2				10ab			PLANTS		TOTAL B's	TOTAL PLANTS	
			l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	1	2	0	WITH	WITH-OUT			
89	MICHOACAN	74	0	0	3	5	5	1	0	2	0	0	0	8	0	0	0	8	0	0	2	6	0	0	8	0	4	0	4	8
90		78	0	0	5	9	9	0	0	5	0	0	0	14	0	0	0	14	0	0	1	13	0	0	14	2	5	4	7	14
91		79	0	0	2	8	10	0	0	0	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
92		105	0	0	4	6	3	2	0	5	0	2	0	8	0	0	0	10	0	0	0	10	0	0	10	1	4	2	5	10
93		186	0	0	2	10	5	2	0	5	0	0	0	12	0	0	0	12	0	0	2	10	0	0	12	2	4	7	6	12
94		191	0	0	4	8	6	2	1	3	0	0	0	12	0	0	0	12	0	0	2	10	0	0	12	1	5	2	6	12
95		199	0	0	0	10	6	0	0	4	1	1	0	8	0	0	0	10	0	0	0	10	1	0	9	0	5	0	5	10
96		200	0	0	2	10	0	6	0	6	2	6	2	2	0	0	0	12	0	0	0	12	0	0	12	0	6	0	6	12
97		204	0	0	0	8	3	2	1	2	0	0	0	8	0	0	0	8	0	0	0	8	1	0	7	0	4	0	4	8
98		211	0	0	1	9	10	0	0	0	0	0	0	10	0	0	0	10	0	0	2	8	0	0	10	0	5	0	5	10
99	MORELOS	1	0	0	6	4	4	4	0	2	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	1	4	1	5	10
100		3	0	0	0	8	4	2	0	2	0	0	0	8	0	0	0	8	0	0	0	8	0	0	8	0	4	0	4	8
101		13	0	0	4	2	3	0	0	3	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	0	3	0	3	6
102		14	0	0	1	7	6	0	0	2	0	1	0	7	0	0	0	8	0	0	0	8	0	0	8	1	3	2	4	8
103		15	0	0	2	4	4	2	0	0	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	0	3	0	3	6
104		17	0	0	2	6	6	1	0	1	0	0	0	8	0	0	0	8	0	0	0	8	2	0	6	1	3	1	4	8
105		18	0	0	3	3	4	1	0	1	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	3	0	7	3	6
106		19	0	0	5	5	7	0	0	3	0	0	0	10	0	0	0	10	0	1	0	9	0	0	10	0	5	0	5	10
107		22	0	0	4	8	6	0	1	5	0	0	0	12	0	0	0	12	0	0	0	12	0	0	12	0	6	0	6	12
108		27	0	0	2	4	4	0	0	2	0	0	0	6	0	0	0	6	0	0	1	5	0	0	6	0	3	0	3	6
109		60	0	0	0	8	5	1	0	2	0	0	0	8	0	0	0	8	0	0	0	8	0	0	8	1	3	2	4	8
110		79	0	0	2	8	7	0	1	2	1	0	0	9	0	0	0	10	0	0	0	10	0	0	10	3	2	6	5	10
111		93	0	0	4	6	6	1	0	3	0	0	0	10	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
112	PUEBLA	33	0	0	0	8	7	0	0	1	0	0	0	8	0	0	0	8	0	1	1	6	1	0	7	0	4	0	4	8
113		196	0	0	2	4	1	3	0	2	0	0	0	6	0	0	0	6	0	0	0	6	1	0	5	1	2	3	3	6
114		200	0	0	2	4	4	2	0	0	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	0	3	0	3	6
115		219	0	0	2	6	5	3	0	0	0	0	0	8	0	0	0	8	0	0	0	8	0	0	8	0	4	0	4	8
116		223	0	0	0	8	5	0	0	3	0	0	0	8	0	0	0	8	0	0	0	8	0	0	8	0	4	0	4	8
117		229	0	0	0	4	5	1	0	0	0	0	0	6	0	0	0	6	0	0	0	6	0	0	6	0	3	0	3	6
118	QUERETARO	1	0	0	0	10	4	0	0	6	0	0	0	10	0	0	0	10	0	4	0	6	0	0	10	5	0	15	5	10
119		4	0	0	0	10	8	1	0	1	0	0	0	10	0	0	0	10	0	0	2	8	0	0	10	5	0	22	5	10
120		15	0	0	2	4	5	0	0	1	3	0	0	3	0	0	0	6	0	2	1	3	0	0	6	2	1	4	3	6
121		20	0	0	0	12	6	1	1	4	0	0	0	12	0	0	0	12	0	0	0	12	3	0	9	0	6	0	6	12
122		29	0	0	0	10	7	0	0	3	0	0	0	10	0	0	0	10	0	0	1	9	0	0	10	0	5	0	5	10
123		31	0	0	0	10	8	1	0	1	0	0	0	10	0	0	0	10	0	1	2	7	0	0	10	3	2	5	5	10
124		34	0	0	2	4	4	0	0	2	0	0	0	6	0	0	0	6	0	0	2	4	0	0	6	2	1	6	3	6
125		39	0	0	0	12	6	1	0	5	4	3	0	5	0	0	0	12	0	0	0	12	0	0	12	3	3	6	6	12
126		43	0	0	0	12	6	0	0	6	3	0	0	9	0	0	0	12	0	0	0	12	0	0	12	0	6	0	6	12
127		48	0	0	1	11	0	5	0	7	0	4	0	8	0	0	0	12	0	0	0	12	0	0	12	0	6	0	6	12
128		49	0	0	0	10	1	1	1	7	4	1	0	5	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
129		50	0	0	0	10	0	2	0	8	0	6	0	4	0	0	0	10	0	0	1	9	0	0	10	0	5	0	5	10
130	S.L.POTOSI	12	0	0	2	8	0	0	1	9	0	0	5	5	0	0	0	10	0	0	0	10	0	0	10	0	5	0	5	10
131		78	0	0	6	6	0	5	0	7	6	2	0	4	0	0	0	12	0	0	0	12	1	0	11	0	6	0	6	12
132		95	0	0	0	6	0	0	0	6	0	3	0	3	0	0	0	6	0	0	1	5	0	0	6	0	3	0	3	6
133		128	0	0	3	9	0	3	2	7	0	3	0	9	0	0	0	12	0	0	0	12	0	0	12	0	6	0	6	12
134		150	0	0	2	10	0	4	3	5	0	3	2	7	0	0	0	12	0	0	2	10	0	0	12	1	5	1	6	12
135	TLAXCALA	1	0	0	0	12	9	0	0	3	0	0	0	12	0	0	0	12	0	0	3	9	0	0	12	0	6	0	6	12
136		3	0	0	0	12	1	4	0	7	0	0	0	12	0	0	0	12	0	0	0	12	1	0	11	0	6	0	6	12
137		5	0	0	0	10	5	0	1	4	0	0	0	10	0	0	0	10	0	0	1	9	0	0	10	2	3	4	5	10
138	VERACRUZ	215	0	0	2	8	0	1	0	9	2	8	0	0	0	0	0	10	0	2	0	8	0	0	10	0	5	0	5	10

TABLE 6. Frequencies for the different knob sizes of the 1S2, 1S1, 1L1, 1L2, 2S2, 2S1, and 2L1 knob positions found in each of the teosinte collections examined from Mexico. The first column, number on map, refers to the numbering of the collections in the collection distribution map given in the text. The small letters l, m, s, and o, indicate large, medium, and small knob sizes and the knobless condition respectively.

NUM. ON MAP	COLLECTION NUMBER	CHROMOSOME KNOB POSITION AND SIZE																												TOTAL NUM CHROM.
		1S2				1S1				1L1				1L2				2S2				2S1				2L1				
		l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	
	CHIHUAHUA																													
1	Nobogame	0	0	0	6	0	0	0	6	0	0	3	3	0	0	0	6	0	0	0	6	0	2	1	3	1	0	0	5	6
2	Nobogame	0	3	0	23	0	0	0	26	0	0	12	14	0	0	0	26	0	0	0	26	2	7	9	8	1	0	0	25	26
	GUANAJUATO																													
3	K-69-2	0	3	3	4	0	0	0	10	4	1	1	4	0	0	2	8	0	0	0	10	0	2	2	6	6	2	0	2	10
4	K-69-10	1	1	0	8	0	0	0	10	5	2	1	2	0	0	3	7	0	0	0	10	5	1	0	4	3	1	0	6	10
5	K-69-11	1	2	1	6	0	0	0	10	1	3	0	6	0	0	0	10	0	0	0	10	3	2	2	3	2	3	2	3	10
6	K-69- 1	0	1	0	9	0	0	0	10	8	0	0	2	0	0	2	8	0	0	0	10	2	0	1	7	4	1	0	5	10
7	K-69- 7	3	0	0	9	0	0	0	12	7	2	0	3	0	0	1	11	0	0	0	12	5	1	0	6	6	2	0	4	12
	GUERRERO																													
8	K-67- 7	5	1	1	9	0	0	0	16	0	2	1	13	0	0	8	8	0	0	0	16	13	0	0	3	11	1	0	4	16
9	K-67- 9	2	1	0	11	0	0	0	14	0	4	4	6	0	0	7	7	0	0	0	14	5	2	1	6	11	0	0	3	14
10	K-67-12	5	5	0	4	0	0	0	14	0	0	3	11	0	0	1	13	0	0	0	14	5	1	0	8	4	2	1	7	14
11	K-67- 8	6	1	1	6	0	0	0	14	0	1	1	12	0	0	6	8	0	0	0	14	9	2	1	2	10	0	0	4	14
12	K-69-13	1	0	0	9	0	0	0	10	1	1	1	7	0	0	0	10	0	0	0	10	3	3	0	4	2	0	0	8	10
13	Beadle '72	1	0	0	3	0	0	0	4	1	0	0	3	0	0	0	4	0	0	0	4	4	0	0	0	1	0	0	3	4
14	Beadle '72	0	0	0	6	0	0	0	6	2	0	0	4	0	0	1	5	0	0	0	6	4	1	0	1	3	0	0	3	6
15	Beadle '72	1	4	1	10	0	0	0	16	4	0	0	12	0	0	1	15	0	0	0	16	11	1	0	4	4	2	0	10	16
16	Wilkes 47711	12	2	0	4	2	2	0	14	0	2	0	16	0	0	7	11	0	0	0	18	10	0	1	7	12	0	0	6	18
17	Wilkes 47335	3	0	0	13	0	0	0	16	1	4	0	11	0	0	3	13	0	0	0	16	10	0	0	6	3	1	0	12	16
	MEXICO																													
18	K-65- 2	4	1	1	2	0	0	0	8	3	0	0	5	0	0	0	8	0	0	0	8	3	1	0	4	8	0	0	0	8
19	K-66- 1	4	0	0	0	0	0	0	4	3	1	0	0	0	0	0	4	0	0	0	4	4	0	0	0	4	0	0	0	4
20	K-67- 1	5	0	0	3	0	0	0	8	8	0	0	0	0	0	0	8	0	0	0	8	6	0	0	2	8	0	0	0	8
21	K-67- 2	3	3	0	2	0	0	1	7	8	0	0	0	0	0	0	8	0	0	0	8	6	0	0	2	6	0	0	2	8
22	K-68- 1	2	4	0	4	0	0	0	10	5	1	1	3	0	0	0	10	0	0	0	10	1	4	1	4	3	1	0	6	10
23	K-68- 2	5	2	0	3	0	0	0	10	8	1	0	1	0	0	0	10	0	0	0	10	6	3	0	1	10	0	0	0	10
24	K-68- 6	3	1	0	2	0	0	0	6	6	0	0	0	0	0	0	6	0	0	0	6	3	1	0	2	5	0	0	1	6
25	K-69-12	9	0	0	3	0	0	0	12	11	0	0	1	0	0	0	12	0	0	0	12	7	2	0	3	12	0	0	0	12
26	K-67- 3	7	1	0	2	0	0	0	10	9	0	0	1	0	0	0	10	0	0	0	10	3	0	1	6	5	0	1	4	10
27	K-68- 4	3	4	1	2	0	0	1	9	9	0	0	1	0	0	1	9	0	0	0	10	9	1	0	0	9	0	0	1	10
28	1970, T-1	12	2	0	6	0	0	0	20	19	0	0	1	0	0	0	20	0	0	0	20	10	2	0	8	16	2	0	2	20
29	1970, T-2	6	6	0	6	0	0	0	18	12	0	1	5	0	0	0	18	0	0	0	18	11	3	0	4	16	0	0	2	18
30	1970, T-3	12	5	0	3	0	0	0	20	14	1	0	5	0	0	0	20	1	0	0	19	11	3	1	5	13	1	0	6	20
31	1970, T-4	11	6	0	5	0	0	1	21	16	4	0	2	0	0	0	22	0	0	0	22	17	0	0	5	19	1	0	2	22
32	K-67-17	0	6	0	4	0	0	0	10	0	0	0	10	0	0	4	6	0	0	0	10	2	1	1	6	1	0	1	8	10
33	K-67-18	2	3	0	7	0	0	0	12	0	0	0	12	0	0	0	12	0	0	0	12	2	1	1	8	3	0	1	8	12
34	K-67-19	1	2	0	9	0	0	0	12	0	0	0	12	0	0	5	7	0	0	0	12	3	1	0	8	2	2	1	7	12
35	K-67-21	3	1	1	5	0	0	0	10	0	0	0	10	0	0	5	5	0	0	0	10	2	1	1	6	2	0	2	6	10
36	K-67-16	7	2	0	1	0	0	0	10	0	0	0	10	0	0	2	8	0	0	0	10	5	3	0	2	0	0	1	9	10
37	K-67-20	4	2	0	4	0	0	0	10	0	0	0	10	0	0	4	6	0	0	0	10	0	3	0	7	1	1	0	8	10
	MICHOACAN																													
38	K-69- 4	0	2	0	2	0	0	0	4	4	0	0	0	0	0	0	4	0	0	0	4	2	1	0	1	3	0	0	1	4
39	K-69- 6	2	3	0	3	0	0	0	8	4	0	0	4	0	0	2	6	0	0	0	8	1	1	0	6	5	0	0	3	8
40	K-69- 8	0	1	0	9	0	0	0	10	3	3	2	2	0	0	1	9	0	0	0	10	2	2	0	6	6	1	0	3	10
41	K-69- 9	2	1	0	11	0	0	0	14	4	3	1	6	0	0	2	12	0	0	0	14	6	2	0	6	5	1	0	8	14
42	K-69- 3	0	0	2	8	0	0	0	10	0	5	0	5	0	0	1	9	0	0	0	10	5	1	0	4	2	1	0	7	10
43	K-69- 5	6	2	0	2	0	0	0	10	10	0	0	0	0	0	3	7	0	0	0	10	4	5	1	0	3	2	0	5	10
44	Wilkes 45470	0	0	0	10	0	0	0	10	6	1	1	2	0	0	2	8	0	0	0	10	4	1	1	4	4	1	0	5	10
45	K-67-14	11	0	0	1	0	0	0	12	0	0	2	10	0	0	6	6	0	0	0	12	5	2	0	5	4	1	0	7	12
46	K-67-13	5	2	0	3	0	0	0	10	0	1	1	8	0	0	1	9	0	0	0	10	2	0	0	8	8	0	0	2	10
47	Wilkes 47942	6	3	0	1	0	0	0	10	2	1	0	7	0	0	0	10	0	0	0	10	1	0	0	9	9	0	0	1	10
48	Wilkes 47890	13	2	0	3	0	0	0	18	0	0	0	18	0	0	3	15	0	0	0	18	13	0	0	5	8	0	0	10	18
49	K-67-15	6	2	0	2	0	0	0	10	10	0	0	0	0	0	3	7	0	0	1	9	4	5	1	0	5	2	0	3	10
50	K-67-23	2	0	3	5	0	0	0	10	0	0	0	10	0	0	2	8	0	0	0	10	0	1	1	8	2	0	0	8	10
51	K-67-25	2	3	0	5	0	0	0	10	0	0	0	10	0	0	1	9	0	0	0	10	1	0	0	9	6	1	0	3	10
52	K-67-24	6	0	2	6	0	0	0	14	0	0	0	14	0	0	0	14	0	0	0	14	4	1	0	9	4	0	0	10	14
53	Wilkes 48897	1	1	0	10	0	0	0	12	6	4	0	2	0	0	1	11	0	0	0	12	7	0	0	5	9	0	0	3	12
54	Wilkes 45085	0	2	2	2	0	0	0	6	0	0	0	6	0	0	3	3	0	0	1	5	2	1	0	3	1	0	0	5	6

TABLE 7. Frequencies for the different knob sizes of the 3S2, 3S1, 3Lo, 3L1, 3L2, 4S2 and 4S1, knob positions found in each of the teosinte collections examined from Mexico. The first column, number on map, refers to the numbering of the collections in the collection distribution map given in the text. The small letters l, m, s, and o, indicate large, medium, and small knob sizes and the knobless condition respectively.

NUM. ON MAP	COLLECTION NUMBER	CHROMOSOME KNOB POSITION AND SIZE																												TOTAL NUM. CHROM.
		3S2				3S1				3Lo				3L1				3L2				4S2				4S1				
		l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	
	CHIHUAHUA																													
1	Noborame	0	0	0	6	0	0	0	6	0	0	0	6	0	0	0	6	0	0	0	6	0	0	0	6	0	0	0	6	6
2	Noborame	0	0	0	26	0	1	0	25	0	0	0	26	1	0	0	25	0	0	0	26	0	0	0	26	0	0	0	26	26
	GUANAJUATO																													
3	K-69- 2	0	0	0	10	0	0	0	10	0	0	0	10	3	7	0	0	0	0	0	10	0	0	0	10	0	0	0	10	10
4	K-69-10	0	0	0	10	0	0	0	10	0	0	0	10	0	1	0	9	0	0	0	10	0	0	0	10	0	0	0	10	10
5	K-69-11	0	1	0	9	0	1	0	9	0	0	0	10	0	3	1	6	0	0	0	10	0	0	0	10	0	0	0	10	10
6	K-69- 1	0	0	0	10	0	0	0	10	0	0	0	10	2	3	0	5	0	0	0	10	0	0	0	10	0	0	0	10	10
7	K-69- 7	0	0	0	12	0	0	0	12	0	0	0	12	11	0	0	1	0	0	0	12	1	0	0	11	0	0	0	12	12
	GUERRERO																													
8	K-67- 7	0	2	6	8	4	4	1	7	0	0	0	16	0	2	1	13	0	0	2	14	4	1	1	10	0	0	0	16	16
9	K-67- 9	0	1	2	11	4	6	0	4	0	0	0	14	7	0	0	7	0	0	0	14	2	3	0	9	0	0	0	14	14
10	K-67-12	0	0	1	13	4	0	2	8	0	0	0	14	1	3	0	10	0	0	0	14	0	4	2	8	0	0	0	14	14
11	K-67- 8	0	0	3	11	2	4	0	8	0	0	0	14	6	4	0	4	0	0	2	12	1	0	0	13	0	0	0	14	14
12	K-69-13	0	0	0	10	0	1	0	9	0	0	0	10	0	1	0	9	0	0	0	10	1	1	1	7	0	0	0	10	10
13	Beadle '72	0	0	0	4	1	0	0	3	0	0	0	4	0	0	0	4	0	0	0	4	3	0	0	1	0	0	0	4	4
14	Beadle '72	0	0	3	3	3	0	0	3	0	0	0	6	4	0	0	2	0	0	0	6	4	1	0	1	0	0	0	6	6
15	Beadle '72	0	0	5	11	9	0	0	7	0	0	0	16	0	1	0	15	0	0	0	16	2	6	1	7	0	0	0	16	16
16	Wilkes 47711	0	0	0	18	1	1	0	16	0	0	0	18	10	2	0	6	0	0	1	17	0	6	0	12	0	0	0	18	18
17	Wilkes 47335	0	0	0	16	5	0	0	11	0	0	0	16	1	0	0	15	0	0	0	16	2	1	0	13	0	0	0	16	16
	MEXICO																													
18	K-65- 2	0	0	0	8	0	2	0	6	0	0	0	8	8	0	0	0	0	0	0	8	0	0	0	8	0	0	0	8	8
19	K-66- 1	0	0	0	4	0	0	0	4	0	0	0	4	4	0	0	0	0	0	0	4	0	0	0	4	0	0	0	4	4
20	K-67- 1	0	0	0	8	0	3	0	5	0	0	0	8	8	0	0	0	0	0	0	8	2	1	0	5	0	0	2	6	8
21	K-67- 2	0	0	0	8	0	2	0	6	0	0	0	8	5	0	0	3	0	0	0	8	1	1	0	6	0	0	2	6	8
22	K-68- 1	0	0	0	10	0	0	0	10	0	0	0	10	6	3	0	1	0	0	0	10	0	0	0	10	0	0	3	7	10
23	K-58- 2	0	0	0	10	0	3	0	7	0	0	1	9	2	5	0	3	0	0	0	10	7	0	0	3	0	0	1	9	10
24	K-58- 6	0	0	0	6	0	0	0	6	0	0	0	6	4	0	0	2	0	0	0	6	3	0	0	3	0	0	2	4	6
25	K-69-12	0	0	0	12	0	2	0	10	0	0	0	12	11	0	0	1	0	0	0	12	4	0	0	8	0	0	0	12	12
26	K-67- 3	0	0	0	10	0	0	0	10	0	0	0	10	10	0	0	0	0	0	0	10	0	0	0	10	0	0	7	3	10
27	K-58- 4	0	0	0	10	0	3	0	7	0	0	0	10	6	1	0	3	0	0	0	10	1	0	0	9	0	0	9	1	10
28	1970, T-1	0	0	0	20	0	0	0	20	0	0	0	20	17	1	1	1	0	0	0	20	0	0	1	19	0	0	0	20	20
29	1970, T-2	0	0	0	18	0	0	0	18	0	0	0	18	16	0	0	2	0	0	0	18	1	1	1	15	0	0	4	14	18
30	1970, T-3	0	0	0	20	0	0	0	20	0	0	0	20	17	0	2	1	0	0	0	20	3	2	0	15	0	0	0	20	20
31	1970, T-4	0	0	0	22	1	6	0	15	0	0	0	22	18	0	0	4	0	0	0	22	9	4	0	9	0	0	1	21	22
32	K-67-17	0	0	0	10	0	1	0	9	0	0	0	10	0	3	0	7	0	0	4	6	0	0	0	10	0	1	0	9	10
33	K-67-18	0	0	1	11	0	2	0	10	0	0	0	12	0	0	0	12	0	0	0	12	0	0	1	11	0	0	0	12	12
34	K-67-19	0	0	0	12	0	2	0	10	0	0	0	12	0	0	0	12	0	0	0	12	0	2	0	10	0	0	0	12	12
35	K-67-21	0	0	0	10	0	1	0	9	0	0	0	10	3	2	0	5	0	0	0	10	0	0	1	9	0	0	0	10	10
36	K-67-16	0	0	0	10	0	2	0	8	0	0	0	10	2	1	0	7	0	0	0	10	0	0	1	9	0	0	0	10	10
37	K-67-20	0	0	0	10	2	3	0	5	0	0	0	10	0	1	0	9	0	0	0	10	0	0	2	8	0	0	0	10	10
	MICHOACAN																													
38	K-69- 4	0	0	0	4	0	0	0	4	0	0	0	4	4	0	0	0	0	0	0	4	0	0	0	4	0	0	0	4	4
39	K-69- 6	0	0	0	8	0	0	0	8	0	0	0	8	8	0	0	0	0	0	0	8	0	0	0	8	0	0	0	8	8
40	K-69- 8	0	0	0	10	0	0	0	10	0	0	0	10	3	4	0	3	0	0	0	10	0	0	0	10	0	0	0	10	10
41	K-69- 9	0	0	0	14	0	1	0	13	0	0	0	14	7	3	0	4	0	0	0	14	0	0	0	14	0	0	0	14	14
42	K-69- 3	0	0	5	5	0	0	0	10	0	0	0	10	1	6	0	3	0	0	0	10	0	0	0	10	0	0	0	10	10
43	K-69- 5	0	0	0	10	2	1	0	7	0	0	0	10	8	1	0	1	0	0	0	10	0	0	0	10	0	0	0	10	10
44	Wilkes 45470	0	0	0	10	0	0	0	10	0	0	1	9	1	0	0	9	0	0	0	10	0	0	0	10	0	0	0	10	10
45	K-67-14	0	0	0	12	0	8	0	4	0	0	1	11	0	2	1	9	0	2	2	8	0	4	3	5	0	0	0	12	12
46	K-67-13	0	0	0	10	7	2	0	1	0	0	0	10	0	1	0	9	0	0	0	10	5	3	0	2	0	0	0	10	10
47	Wilkes 47942	0	0	0	10	9	0	0	1	0	0	1	9	0	0	0	10	0	0	0	10	1	7	1	1	0	0	0	10	10
48	Wilkes 47890	0	0	0	18	10	0	0	8	0	0	0	18	1	2	0	15	0	0	7	11	1	1	4	12	0	0	0	18	18
49	K-67-15	0	0	0	10	2	1	0	7	0	0	0	10	8	1	0	1	0	0	0	10	0	0	0	10	0	0	0	10	10
50	K-67-23	0	0	0	10	2	0	0	8	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	0	0	0	10	10
51	K-67-25	0	0	2	8	0	0	1	9	0	0	0	10	0	3	0	7	0	0	0	10	0	0	0	10	0	0	0	10	10
52	K-67-24	0	0	0	14	1	0	1	12	0	0	0	14	0	0	0	14	0	0	1	13	0	0	2	12	0	0	0	14	14
53	Wilkes 48597	0	0	0	12	0	0	0	12	0	0	0	12	12	0	0	0	0	0	0	12	0	0	0	12	0	0	0	12	12
54	Wilkes 48085	0	0	0	6	2	0	0	4	0	0	0	6	0	0	0	6	0	0	0	6	0	0	1	5	0	0	0	6	6

TABLE 8. Frequencies for the different knob sizes of the 4L1, 4L2, 5S2, 5S1, 5L1, 6L1, and 6L2, knob positions found in each of the teosinte collections examined from Mexico. The first column, number on map, refers to the numbering of the collections in the collection distribution map given in the text. The small letters l, m, s, and o, indicate large, medium, and small knob sizes and the knobless condition respectively.

NUM. ON MAP	COLLECTION NUMBER	CHROMOSOME KNOB POSITION AND SIZE																												TOTAL
		4L1				4L2				5S2				5S1				5L1				6L1				6L2				NUM.
		l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	CHROM.
	CHIHUAHUA																													
1	Nobogame	1	0	2	3	0	0	0	6	0	0	0	6	0	0	0	6	1	0	0	5	0	0	0	6	0	0	3	3	6
2	Nobogame	3	3	13	7	0	0	0	26	0	0	0	26	0	0	0	26	4	0	2	20	0	0	0	26	1	0	3	22	26
	GUANAJUATO																													
3	K-69- 2	7	1	0	2	0	0	0	10	0	0	0	10	0	0	0	10	8	1	0	1	0	2	0	8	0	0	3	7	10
4	K-69-10	5	1	0	4	0	0	0	10	0	0	0	10	0	0	0	10	7	0	0	3	0	1	0	9	0	0	3	7	10
5	K-69-11	6	3	0	1	0	0	0	10	0	0	0	10	0	0	0	10	4	3	0	3	0	0	0	10	0	0	2	8	10
6	K-69- 1	8	0	0	2	0	0	0	10	0	0	0	10	0	0	0	10	7	0	0	3	3	1	0	6	0	0	0	10	10
7	K-69- 7	9	2	0	1	0	0	0	12	0	0	0	12	0	0	0	12	12	0	0	0	0	0	0	12	0	0	4	8	12
	GUERRERO																													
8	K-67- 7	4	4	2	6	0	0	0	16	0	0	0	16	0	0	0	16	9	3	0	4	0	0	0	16	0	1	9	6	16
9	K-67- 9	12	0	0	2	0	0	0	14	0	0	0	14	1	0	0	13	12	0	0	2	0	0	0	14	0	0	8	6	14
10	K-67-12	12	0	0	2	0	0	0	14	0	1	0	13	0	0	0	14	8	4	0	2	0	0	0	14	0	0	8	6	14
11	K-67- 8	8	1	0	5	0	0	0	14	0	0	0	14	0	0	0	14	14	0	0	0	0	0	0	14	0	5	4	5	14
12	K-69-13	4	0	1	5	0	0	0	10	0	0	0	10	1	0	0	9	7	1	0	2	0	0	0	10	0	0	1	9	10
13	Beadle ·72	2	0	0	2	0	0	0	4	0	0	0	4	2	0	0	2	2	0	0	2	0	0	0	4	0	0	2	2	4
14	Beadle ·72	1	0	0	5	0	0	0	6	0	0	0	6	1	0	0	5	4	0	0	2	0	0	0	6	0	0	4	2	6
15	Beadle ·72	3	4	0	9	0	0	0	16	0	0	0	16	1	0	0	15	14	0	0	2	0	0	1	15	0	0	8	8	16
16	Wilkes 47711	13	1	0	4	0	0	0	18	0	0	0	18	1	0	0	17	14	3	0	1	0	0	0	18	0	0	13	5	18
17	Wilkes 47335	3	1	0	12	0	0	0	16	0	0	0	16	2	0	0	14	10	0	0	6	0	0	0	16	0	0	6	10	16
	MEXICO																													
18	K-65- 2	8	0	0	0	0	0	0	8	0	0	0	8	3	0	0	5	5	0	0	3	8	0	0	0	0	0	0	8	8
19	K-66- 1	2	1	0	1	0	0	0	4	0	0	0	4	2	1	0	1	4	0	0	0	4	0	0	0	0	0	0	4	4
20	K-67- 1	3	3	0	2	0	0	0	8	0	0	0	8	1	1	0	6	8	0	0	0	7	0	0	1	0	0	2	6	8
21	K-67- 2	8	0	0	0	0	0	0	8	0	0	0	8	6	0	0	2	8	0	0	0	5	0	1	2	0	0	1	7	8
22	K-65- 1	4	3	0	3	0	0	0	10	0	0	0	10	4	2	0	4	10	0	0	0	4	2	0	4	0	0	3	7	10
23	K-68- 2	4	4	0	2	0	0	0	10	0	0	0	10	2	1	0	7	5	4	0	1	10	0	0	0	0	0	5	5	10
24	K-65- 6	4	0	0	2	0	0	0	6	0	0	0	6	0	4	0	2	6	0	0	0	5	0	0	1	0	0	0	6	6
25	K-69-12	11	0	0	1	0	0	0	12	0	0	0	12	8	0	0	4	10	0	0	2	10	0	0	2	0	0	1	11	12
26	K-67- 3	8	1	0	1	0	0	0	10	0	0	0	10	1	0	0	9	5	3	0	2	3	2	1	4	0	0	3	7	10
27	K-68- 4	8	1	0	1	0	0	0	10	0	0	0	10	5	2	1	2	8	0	0	2	9	0	0	1	0	0	3	7	10
28	1970, T-1	15	1	0	4	0	0	0	20	0	0	0	20	5	2	0	13	17	1	0	2	9	5	0	6	0	0	4	16	20
29	1970, T-2	18	0	0	0	0	0	0	18	0	0	0	18	4	0	0	14	13	2	0	3	18	0	0	0	0	0	5	13	18
30	1970, T-3	17	0	0	3	0	0	0	20	0	0	0	20	5	4	0	11	13	6	0	1	18	0	0	2	0	0	1	19	20
31	1970, T-4	18	1	0	3	0	0	0	22	0	0	0	22	15	3	0	4	21	0	0	1	17	2	0	3	0	0	3	19	22
32	K-67-17	7	1	0	2	0	0	0	10	0	0	0	10	0	0	0	10	7	0	0	3	0	0	0	10	0	0	4	6	10
33	K-67-18	5	2	0	5	0	0	0	12	0	0	0	12	0	1	0	11	3	1	0	8	0	0	0	12	0	2	3	7	12
34	K-67-19	3	3	0	6	0	0	0	12	0	0	0	12	0	0	0	12	9	0	0	3	0	0	0	12	0	0	5	7	12
35	K-67-21	7	0	0	3	0	0	0	10	0	0	0	10	0	0	0	10	6	1	0	3	0	0	0	10	0	0	3	7	10
36	K-67-16	6	0	0	4	0	0	0	10	0	0	0	10	0	0	0	10	5	2	0	3	0	0	0	10	0	0	7	3	10
37	K-67-20	5	2	0	3	0	0	0	10	0	0	0	10	0	0	0	10	7	1	0	2	0	0	0	10	0	1	3	6	10
	MICHOACAN																													
38	K-69- 4	2	0	0	2	0	0	0	4	0	0	0	4	0	0	0	4	4	0	0	0	1	0	0	3	0	0	0	4	4
39	K-69- 6	8	0	0	0	0	0	0	8	0	0	0	8	0	0	0	8	7	0	0	1	1	0	0	7	0	0	1	7	8
40	K-69- 8	8	1	0	1	0	0	0	10	0	0	0	10	0	0	0	10	6	0	0	4	0	2	0	8	0	0	5	5	10
41	K-69- 9	8	0	0	6	0	0	0	14	0	0	0	14	0	0	0	14	13	0	0	1	4	2	0	8	0	1	2	11	14
42	K-69- 3	2	4	0	4	0	0	0	10	0	0	0	10	0	0	0	10	2	8	0	0	0	0	0	10	0	0	5	5	10
43	K-69- 5	3	5	1	1	0	0	0	10	0	0	0	10	0	0	0	10	7	2	0	1	4	2	0	4	0	0	2	8	10
44	Wilkes 45470	9	0	0	1	0	0	0	10	0	0	0	10	0	0	0	10	10	0	0	0	9	0	0	1	0	0	7	3	10
45	K-67-14	11	0	0	1	0	0	0	12	0	0	0	12	0	0	0	12	10	1	0	1	0	0	0	12	0	3	5	4	12
46	K-67-13	9	0	0	1	0	0	0	10	0	0	0	10	1	0	0	9	9	1	0	0	0	0	0	10	0	0	8	2	10
47	Wilkes 47942	9	0	0	1	0	0	0	10	0	0	0	10	0	0	0	10	8	0	0	2	0	0	0	10	0	0	5	5	10
48	Wilkes 47890	15	0	0	3	0	0	0	18	0	0	0	18	0	0	0	18	18	0	0	0	0	0	0	18	0	0	12	6	18
49	K-67-15	3	5	1	1	0	0	0	10	0	0	0	10	0	0	0	10	7	2	0	1	3	2	0	5	0	0	2	8	10
50	K-67-23	5	2	0	3	0	0	0	10	0	0	0	10	0	0	0	10	7	1	0	2	0	0	0	10	0	0	5	5	10
51	K-67-25	4	4	0	2	0	1	0	9	0	0	0	10	0	0	0	10	8	1	0	1	0	0	0	10	0	0	5	5	10
52	K-67-24	8	1	0	5	0	0	0	14	0	0	0	14	0	1	0	13	10	0	0	4	0	0	0	14	0	2	4	8	14
53	Wilkes 48897	10	0	0	2	0	0	0	12	0	0	0	12	7	0	0	5	12	0	0	0	0	0	0	12	0	2	7	3	12
54	Wilkes 48085	3	0	0	3	0	0	0	6	0	0	0	6	0	0	0	6	5	0	0	1	0	0	0	6	0	0	5	1	6

TABLE 9. Frequencies for the different knob sizes of the 6L3, 6L4, 7S, 7L1, 7L2, 8S, and 8L1, knob positions found in each of the teosinte collections examined from Mexico. The fifst column, number on map, refers to the numbering of the collections in the collection distribution map given in the text. The small letters l, m, s, and o, indicate large, medium, and small knob sizes and the knobless condition respectively.

NUM. ON MAP	COLLECTION NUMBER	CHROMOSOME KNOB POSITION AND SIZE																												TOTAL NUM. CHROM.
		6L3				6L4				7S				7L1				7L2				8S				8L1				
		l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	
	CHIHUAHUA																													
1	Nobogame	0	0	0	6	0	0	0	6	0	0	0	6	0	0	0	6	0	0	0	6	0	0	0	6	0	0	0	6	6
2	Nobogame	0	0	2	24	0	0	0	26	0	0	0	26	0	0	0	26	0	0	0	26	0	0	0	26	0	0	0	26	26
	GUANAJUATO																													
3	K-69- 2	0	0	2	8	0	0	0	10	0	0	0	10	0	8	0	2	0	0	0	10	0	0	0	10	5	1	0	4	10
4	K-69-10	0	0	1	9	0	0	0	10	0	0	0	10	3	1	0	6	0	0	0	10	0	0	0	10	2	0	0	8	10
5	K-69-11	0	5	2	3	0	0	0	10	0	0	0	10	2	1	0	7	0	0	2	8	0	0	0	10	2	4	1	3	10
6	K-69- 1	0	0	4	6	0	0	0	10	1	0	0	9	3	1	0	6	0	0	0	10	0	0	0	10	1	3	0	6	10
7	K-69- 7	0	1	3	8	0	0	0	12	0	0	0	12	7	0	1	4	0	0	0	12	0	0	0	12	4	3	0	5	12
	GUERRERO																													
8	K-67- 7	0	5	4	7	0	0	4	12	0	1	0	15	11	1	0	4	0	0	10	6	0	0	3	13	12	1	0	3	16
9	K-67- 9	0	6	3	5	0	2	2	10	0	0	0	14	13	0	0	1	0	0	2	12	0	0	1	13	9	2	0	3	14
10	K-67-12	4	4	1	5	0	0	0	14	2	3	0	9	12	0	0	2	0	0	2	12	0	0	0	14	10	1	0	3	14
11	K-67- 8	3	2	3	6	0	0	1	13	1	1	0	12	11	0	0	3	0	0	8	6	0	0	2	12	11	0	0	3	14
12	K-69-13	9	0	0	1	0	0	0	10	0	1	0	9	10	0	0	0	0	0	0	10	0	0	0	10	2	3	0	5	10
13	Beadle :72	4	0	0	0	0	0	0	4	0	0	0	4	4	0	0	0	0	0	0	4	0	0	0	4	3	0	0	1	4
14	Beadle '72	6	0	0	0	0	0	0	6	0	1	0	5	4	0	0	2	0	0	0	6	0	0	0	6	5	0	0	1	6
15	Beadle '72	13	2	0	1	0	0	0	16	0	0	0	16	15	0	0	1	0	0	1	15	0	0	1	15	12	1	1	2	16
16	Wilkes 47711	9	6	2	1	0	0	1	17	0	1	0	17	14	0	0	4	0	0	0	18	0	0	0	18	15	2	0	1	18
17	Wilkes 47335	8	2	0	6	0	0	0	16	0	0	1	15	12	0	0	4	0	0	0	16	0	0	2	14	5	3	0	8	16
	MEXICO																													
18	K-65- 2	0	0	1	7	0	0	0	8	2	1	0	5	8	0	0	0	0	0	0	8	0	0	0	8	7	0	0	1	8
19	K-66- 1	0	0	1	3	0	0	0	4	3	0	0	1	4	0	0	0	0	0	0	4	0	0	0	4	4	0	0	0	4
20	K-67- 1	0	0	0	8	0	0	0	8	0	0	0	8	7	0	0	1	0	0	0	8	0	0	0	8	8	0	0	0	8
21	K-67- 2	0	0	1	7	0	0	0	8	1	2	0	5	7	0	0	1	0	0	0	8	0	0	0	8	7	0	0	1	8
22	K-68- 1	0	0	0	10	0	0	0	10	0	0	3	7	5	3	0	2	0	0	0	10	0	0	0	10	0	7	0	3	10
23	K-68- 2	0	0	0	10	0	0	0	10	2	0	0	8	5	3	0	2	0	0	0	10	0	0	0	10	4	2	0	4	10
24	K-68- 6	0	0	4	2	0	0	0	6	5	0	0	1	5	0	0	1	0	0	0	6	0	0	0	6	6	0	0	0	6
25	K-69-12	0	0	0	12	0	0	0	12	6	1	1	4	12	0	0	0	0	0	0	12	0	0	0	12	9	0	0	3	12
26	K-67- 3	0	0	0	10	0	0	0	10	0	0	1	9	7	2	0	1	0	0	0	10	0	0	0	10	3	2	0	5	10
27	K-68- 4	0	0	0	10	0	0	0	10	0	6	0	4	3	6	0	1	0	0	0	10	0	0	0	10	6	1	0	3	10
28	1970, T-1	0	0	3	17	0	0	0	20	2	2	1	15	16	3	0	1	0	0	0	20	0	0	0	20	16	1	0	3	20
29	1970, T-2	0	0	1	17	0	0	0	18	5	5	0	8	16	0	0	2	0	0	0	18	0	0	0	18	16	0	0	2	18
30	1970, T-3	0	0	2	18	0	0	0	20	7	6	0	7	20	0	0	0	0	0	0	20	0	0	0	20	18	0	0	2	20
31	1970, T-4	0	0	7	15	0	0	0	22	9	4	0	9	16	3	0	3	0	0	0	22	0	0	0	22	20	1	0	1	22
32	K-67-17	0	4	2	4	0	0	0	10	0	3	0	7	2	2	1	5	0	0	5	5	0	0	0	10	0	4	1	5	10
33	K-67-18	0	2	4	6	0	0	0	12	1	2	0	9	0	3	1	8	0	0	4	8	0	1	4	7	2	2	0	8	12
34	K-67-19	2	2	3	5	0	0	0	12	0	4	0	8	1	3	0	8	0	0	1	11	0	0	1	11	1	1	2	8	12
35	K-67-21	2	3	0	5	0	0	0	10	3	1	2	4	6	1	0	3	0	0	1	9	0	0	3	7	6	1	0	3	10
36	K-67-16	5	3	1	1	0	0	0	10	2	0	0	8	2	1	0	7	0	0	3	7	0	0	0	10	2	1	1	6	10
37	K-67-20	0	1	3	6	0	0	0	10	0	1	1	8	4	3	0	3	0	0	3	7	0	0	1	9	0	3	0	7	10
	MICHOACAN																													
38	K-69- 4	0	1	0	3	0	0	0	4	0	0	0	4	1	0	0	3	0	0	0	4	0	0	0	4	0	2	0	2	4
39	K-69- 6	0	2	2	4	0	0	0	8	0	1	0	7	7	0	0	1	0	0	3	5	0	0	0	8	4	0	0	4	8
40	K-69- 8	0	0	0	10	0	0	0	10	0	0	0	10	3	1	0	6	0	0	0	10	0	0	0	10	3	1	0	6	10
41	K-69- 9	0	2	5	7	0	0	0	14	2	0	0	12	5	2	0	7	0	0	1	13	0	1	0	13	5	0	0	9	14
42	K-69- 3	0	3	3	4	0	0	0	10	0	0	0	10	1	0	0	9	0	0	0	10	0	0	0	10	0	4	1	5	10
43	K-69- 5	0	1	2	7	0	0	0	10	0	1	0	9	10	0	0	0	0	0	3	7	0	0	1	9	0	1	0	9	10
44	Wilkes 45470	0	0	0	10	0	0	0	10	0	0	0	10	2	0	0	8	0	0	1	9	0	0	0	10	3	0	0	7	10
45	K-67-14	4	6	1	1	0	0	0	12	4	1	3	4	0	3	0	9	0	0	3	9	0	0	7	5	7	1	1	3	12
46	K-67-13	8	0	0	2	0	0	0	10	3	0	1	6	2	2	0	6	0	0	0	10	0	0	0	10	6	2	0	2	10
47	Wilkes 47942	9	1	0	0	0	0	0	10	5	2	2	1	3	0	2	5	0	0	0	10	0	0	1	9	9	0	0	1	10
48	Wilkes 47890	3	9	0	6	0	0	0	18	10	1	1	6	4	3	0	11	0	4	0	14	0	3	7	8	8	5	0	5	18
49	K-67-15	1	1	2	6	0	0	0	10	0	1	0	9	10	0	0	0	0	0	3	7	0	0	1	9	0	1	0	9	10
50	K-67-23	0	0	4	6	0	0	0	10	0	1	0	9	4	0	0	6	0	0	2	8	0	0	0	10	5	1	0	4	10
51	K-67-25	0	1	4	5	0	0	0	10	0	1	0	9	1	0	1	8	0	0	0	10	0	0	0	10	1	3	0	6	10
52	K-67-24	1	1	0	12	0	0	0	14	0	2	6	6	4	0	0	10	0	0	6	8	0	0	3	11	10	1	0	3	14
53	Wilkes 48897	0	0	0	12	0	0	0	12	0	0	0	12	8	0	0	4	0	0	0	12	0	0	0	12	8	0	1	3	12
54	Wilkes 48085	3	0	2	1	0	0	0	6	0	5	0	1	0	1	0	5	0	0	1	5	0	0	0	6	5	0	0	1	6

TABLE 10. Frequencies for the different knob sizes of the 8L2, 9S, 9L1, 9L2, 10L1, and 10L2, knob positions and of the type I and II of the abnormal chromosome 10 (10 ab) and B chromosomes found in each of the teosinte collections examined from Mexico. The first column, number on map, refers to the numbering of the collections in the collection distribution map given in the text. The small letters l, m, s, and o, indicate large, medium, and small knob sizes and the knobless condition respectively.

NUM. ON MAP	COLLECTION NUMBER	CHROMOSOME KNOB POSITION AND SIZE																								B CHROMOSOME				TOTAL NUM. CHROM.
		8L2				9S				9L1			9L2				10L1			10L2			10 ab			PLANTS		TOTAL B'S	TOTAL PLANTS	
		l	m	s	o	l	m	s	o	m	s	o	l	m	s	o	m	s	o	m	s	o	1	2	o	WITH	WITHOUT			
	CHIHUAHUA																													
1	Nobogame	0	0	0	6	0	0	0	6	0	0	6	0	0	0	6	0	0	6	0	0	6	0	0	6	0	3	0	3	6
2	Nobogame	0	0	1	25	2	0	1	23	0	0	26	0	0	0	26	0	0	26	0	0	26	0	0	26	0	13	0	13	26
	GUANAJUATO																													
3	K-69- 2	0	0	7	3	3	2	0	5	0	2	8	0	3	1	6	2	0	8	0	0	10	0	0	10	0	5	0	5	10
4	K-69-10	0	1	4	5	1	1	0	8	0	0	10	2	0	0	8	2	0	8	0	0	10	0	0	10	1	4	1	5	10
5	K-69-11	0	0	6	4	0	0	1	9	0	0	10	0	3	2	5	0	1	9	0	0	10	0	0	10	1	4	1	5	10
6	K-69- 1	0	0	3	7	4	0	0	6	0	0	10	0	2	0	8	0	0	10	0	0	10	0	0	10	0	5	0	5	10
7	K-69- 7	0	0	6	6	2	1	0	9	0	2	10	2	2	0	8	1	0	11	0	1	11	0	2	10	3	3	4	6	12
	GUERRERO																													
8	K-67- 7	0	0	10	6	10	1	1	4	0	0	16	3	3	0	10	1	0	15	1	0	15	0	1	15	0	8	0	8	16
9	K-67- 9	0	0	9	5	4	5	0	5	0	0	14	3	4	0	7	0	1	13	1	3	10	0	1	13	0	7	0	7	14
10	K-67-12	0	3	5	6	9	0	2	3	0	0	14	0	1	0	13	0	0	14	0	1	13	0	1	13	0	7	0	7	14
11	K-67- 8	0	0	7	7	9	0	3	2	0	0	14	0	2	0	12	0	0	14	4	0	10	0	1	13	0	7	0	7	14
12	K-69-13	0	0	3	7	5	2	0	3	0	0	10	0	0	0	10	1	0	9	0	0	10	0	0	10	0	5	0	5	10
13	Beadle '72	0	0	2	2	3	0	0	1	0	0	4	0	0	0	4	0	0	4	0	0	4	0	0	4	1	1	1	2	4
14	Beadle '72	0	0	1	5	4	0	0	2	0	0	6	0	0	0	6	0	0	6	0	0	6	0	1	5	0	3	0	3	6
15	Beadle '72	0	0	7	9	8	5	1	2	0	0	16	1	0	0	15	0	0	16	0	0	16	0	4	12	0	8	0	8	16
16	Wilkes 47711	0	0	5	13	6	4	2	6	0	0	18	0	2	0	16	0	0	18	0	1	17	0	1	17	0	9	0	9	18
17	Wilkes 47335	0	0	2	14	7	0	1	8	0	0	16	1	0	0	15	1	0	15	0	0	16	0	0	16	7	1	17	8	16
	MEXICO																													
18	K-65- 2	0	0	1	7	4	1	0	3	0	0	8	0	0	0	8	0	0	8	0	1	7	0	0	8	0	4	0	4	8
19	K-66- 1	0	0	0	4	4	0	0	0	0	0	4	0	0	0	4	0	0	4	0	0	4	0	1	3	0	2	0	2	4
20	K-67- 1	0	0	2	6	7	0	0	1	0	0	8	0	0	0	8	1	2	5	0	1	7	0	0	8	0	4	0	4	8
21	K-67- 2	0	0	0	8	5	0	0	3	0	0	8	0	0	0	8	0	0	8	0	0	8	0	2	6	0	4	0	4	8
22	K-68- 1	0	0	0	10	3	3	0	4	0	0	10	0	0	0	10	0	0	10	0	6	4	0	0	10	0	5	0	5	10
23	K-68- 2	0	0	1	9	10	0	0	0	0	0	10	0	0	0	10	0	0	10	0	4	6	0	0	10	0	5	0	5	10
24	K-68- 6	0	0	0	6	2	1	0	3	0	0	6	0	0	0	6	0	0	6	0	1	5	0	3	3	0	3	0	3	6
25	K-69-12	0	0	0	12	8	0	0	4	0	0	12	0	0	0	12	0	0	12	0	0	12	0	0	12	0	6	0	6	12
26	K-67- 3	0	0	0	10	0	1	0	9	0	0	10	0	0	0	10	0	0	10	0	0	10	0	0	10	0	5	0	5	10
27	K-68- 4	0	0	1	9	2	4	1	3	0	0	10	0	0	0	10	0	0	10	0	5	5	0	0	10	0	5	0	5	10
28	1970, T-1	0	0	0	20	11	0	2	7	0	0	20	0	0	0	20	0	2	18	0	3	17	0	0	20	0	10	0	10	20
29	1970, T-2	0	0	0	18	11	2	0	5	0	0	18	0	0	0	18	0	0	18	0	4	14	0	1	17	0	9	0	9	18
30	1970, T-3	0	0	0	20	7	0	2	11	0	0	20	0	0	0	20	1	2	17	0	2	18	0	1	19	0	10	0	10	20
31	1970, T-4	0	0	4	18	12	1	0	9	0	0	22	0	0	0	22	0	0	22	0	1	21	0	3	19	0	11	0	11	22
32	K-67-17	0	0	2	8	5	2	2	1	0	0	10	0	2	0	8	0	0	10	0	0	10	0	0	10	0	5	0	5	10
33	K-67-18	0	0	4	8	8	1	0	3	0	0	12	0	0	0	12	0	0	12	0	0	12	2	0	10	0	6	0	6	12
34	K-67-19	0	2	4	6	7	1	0	4	0	0	12	0	0	0	12	0	0	12	0	0	12	0	0	12	0	6	0	6	12
35	K-67-21	0	0	6	4	6	0	2	2	0	0	10	0	1	2	7	1	0	9	0	1	9	1	0	9	0	5	0	5	10
36	K-67-16	0	2	5	3	6	1	0	3	0	0	10	0	0	0	10	0	0	10	0	0	10	0	0	10	0	5	0	5	10
37	K-67-20	0	0	4	6	6	0	0	4	0	0	10	0	1	0	9	0	0	10	0	0	10	0	0	10	0	5	0	5	10
	MICHOACAN																													
38	K-69- 4	0	0	3	1	0	0	0	4	0	0	4	0	1	0	3	0	0	4	0	0	4	0	0	4	0	2	0	2	4
39	K-69- 6	0	0	2	6	0	1	0	7	0	0	8	1	2	1	4	1	0	7	0	1	7	0	0	8	1	3	3	4	8
40	K-69- 8	0	0	5	5	2	2	0	6	0	0	10	0	0	0	10	3	0	7	0	0	10	0	0	10	0	5	0	5	10
41	K-69- 9	0	1	6	7	2	2	0	10	0	4	10	2	1	1	10	0	0	14	2	0	12	0	0	14	0	7	0	7	14
42	K-69- 3	0	0	6	4	2	0	4	4	0	0	10	2	3	2	3	1	0	9	0	0	10	0	0	10	0	5	0	5	10
43	K-69- 5	0	0	8	2	0	2	3	5	0	4	6	2	0	2	6	2	0	8	0	1	9	0	0	10	1	4	1	5	10
44	Wilkes 45470	0	0	8	2	0	1	2	7	0	2	8	5	2	0	3	0	0	10	0	0	10	0	0	10	0	5	0	5	10
45	K-67-14	0	0	3	9	8	2	0	2	0	0	12	0	0	0	12	2	0	10	0	1	11	1	0	11	0	6	0	6	12
46	K-67-13	0	0	2	8	8	0	1	1	0	0	10	0	0	0	10	0	0	10	0	0	10	0	0	10	0	5	0	5	10
47	Wilkes 47942	0	0	3	7	9	1	0	0	0	0	10	0	0	2	8	0	0	10	0	0	10	0	0	10	1	4	2	5	10
48	Wilkes 47890	0	0	8	10	15	0	0	3	0	0	18	0	0	0	18	0	0	18	0	0	18	1	0	17	3	6	6	9	18
49	K-67-15	0	0	8	2	0	2	3	5	0	2	8	2	0	3	5	2	0	8	0	1	9	0	0	10	1	4	1	5	10
50	K-67-23	0	0	3	7	5	3	0	2	0	0	10	0	0	1	9	0	1	9	0	0	10	0	0	10	0	5	0	5	10
51	K-67-25	0	1	5	4	7	1	0	2	0	0	10	0	0	0	10	0	1	9	0	0	10	0	0	10	1	4	3	5	10
52	K-67-24	0	0	7	7	11	1	1	1	0	0	14	0	0	0	14	0	0	14	0	1	13	1	0	13	0	7	0	7	14
53	Wilkes 48897	0	0	7	5	0	0	0	12	0	0	12	0	0	0	12	8	0	4	0	0	12	0	0	12	0	6	0	6	12
54	Wilkes 45085	0	0	1	5	3	0	1	2	0	0	6	0	0	0	6	0	1	5	0	0	6	0	0	6	0	3	0	3	6

TABLE 11. Frequencies for the different knob sizes of the terminal knobpositions found in each of the teosinte collections examined from northern and southern Guatemala. The first column, number on map, refers to the numbering of the collections in the collection distribution map given in the text. The small letters l, m, s, and o, indicate large, medium, and small knob sizes and the knobless condition respectively.

NUM. ON MAP	COLLECTION NUMBER	CHROMOSOME KNOB POSITION AND SIZE																																							
		1S3				1L3				2S3				2L2				3S2				3L3				4S2				4L3				5S2				5L2			
		l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o
	SOUTHERN GUATEMALA																																								
	Chiquimula																																								
55	Wilkes 51850	0	1	2	1	0	0	0	4	1	2	0	1	0	3	0	1	3	1	0	0	0	0	0	4	4	0	0	0	0	0	3	1	3	0	0	1	1	1	0	2
	Jutiapa																																								
56	Wilkes 51839	6	3	0	3	0	0	0	12	7	4	0	1	7	0	0	5	0	0	0	12	0	0	0	12	5	1	4	2	1	10	0	1	9	0	0	3	0	4	0	8
57	Wilkes 51764	1	4	0	5	0	0	0	10	7	2	0	1	3	2	3	2	4	1	0	5	0	0	0	10	7	1	0	2	0	5	2	3	7	2	0	1	1	3	0	6
58	Cutler 202 A	4	4	0	2	0	0	0	10	6	1	0	3	7	0	1	2	5	3	0	2	0	0	0	10	7	0	0	3	1	6	0	3	6	0	1	3	7	0	0	3
	NORTHERN GUATEMALA																																								
	Huehuetenango																																								
59	San Antonio Huixta	1	4	0	1	0	0	0	6	3	1	1	1	0	4	0	2	4	1	0	1	0	0	2	4	0	0	3	3	0	1	3	2	4	0	0	2	0	0	3	3
60	Tzisbaj	6	16	0	4	0	0	1	25	8	6	3	9	1	4	12	9	16	2	1	7	0	2	5	19	0	2	19	5	2	7	8	9	16	6	1	3	0	0	14	12
61	Nomajil	6	7	1	6	0	0	0	20	12	1	4	3	0	0	7	13	8	3	2	7	0	0	4	16	0	1	13	6	3	5	3	9	17	0	0	3	0	0	11	9

NUM. ON MAP	COLLECTION NUMBER	CHROMOSOME KNOB POSITION AND SIZE																																			TOTAL NUM. CHROM.
		6L5				7S				7L3				8S				8L3				9S				9L3				10S				10L3				
		l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	
	SOUTHERN GUATEMALA																																					
	Chiquimula																																					
55	Wilkes 51850	4	0	0	0	0	0	0	4	1	1	0	2	0	0	0	4	2	0	0	2	0	0	0	4	0	0	4	0	0	0	0	4	3	1	0	0	4
	Jutiapa																																					
56	Wilkes 51839	3	5	0	4	0	0	0	12	2	2	3	5	0	0	0	12	9	0	0	3	0	0	0	12	7	2	1	2	0	0	0	12	12	0	0	0	12
57	Wilkes 51764	5	4	0	1	0	0	0	10	1	0	0	9	0	0	0	10	6	0	0	4	0	0	0	10	8	1	1	0	0	0	0	10	7	0	0	3	10
58	Cutler 202 A	2	4	0	4	0	0	0	10	2	1	4	3	0	0	0	10	9	0	0	1	0	0	0	10	8	1	0	1	0	0	0	10	7	0	2	1	10
	NORTHERN GUATEMALA																																					
	Huehuetenango																																					
59	San Antonio Huixta	0	3	1	2	0	4	0	2	0	1	3	2	4	0	0	2	1	0	0	5	4	0	0	2	0	0	2	4	0	0	0	6	0	0	2	4	6
60	Tzisbaj	0	5	14	7	17	2	4	3	0	0	17	9	14	7	1	4	0	1	1	24	17	1	2	6	0	0	0	26	0	0	0	26	0	0	13	13	26
61	Nomajil	1	2	10	7	3	3	1	13	0	0	14	6	14	4	8	0	0	1	4	15	8	5	0	7	0	0	0	20	0	0	0	20	0	0	9	11	20

FIGURES 1 to 16. Geographical distribution of the relative frequencies of the several knob sizes [large, medium, small and knobless] found at different knob positions in collections of Mexican teosinte.

In each figure, the maps illustrate the distribution of: A. large knobs; B. medium knobs; C. small knobs; and D. knobless. Each circle represents a single collection. Black circles represent high frequencies [more than 2/3 of the total number of chromosomes of each collection]; half circles represent intermediate frequencies [1/3 to 2/3 of the total chromosomes]; open circles represent low frequencies [less than 1/3 of the total chromosomes]; and the X's represent absence of the particular knob condition that the specific map is considering.

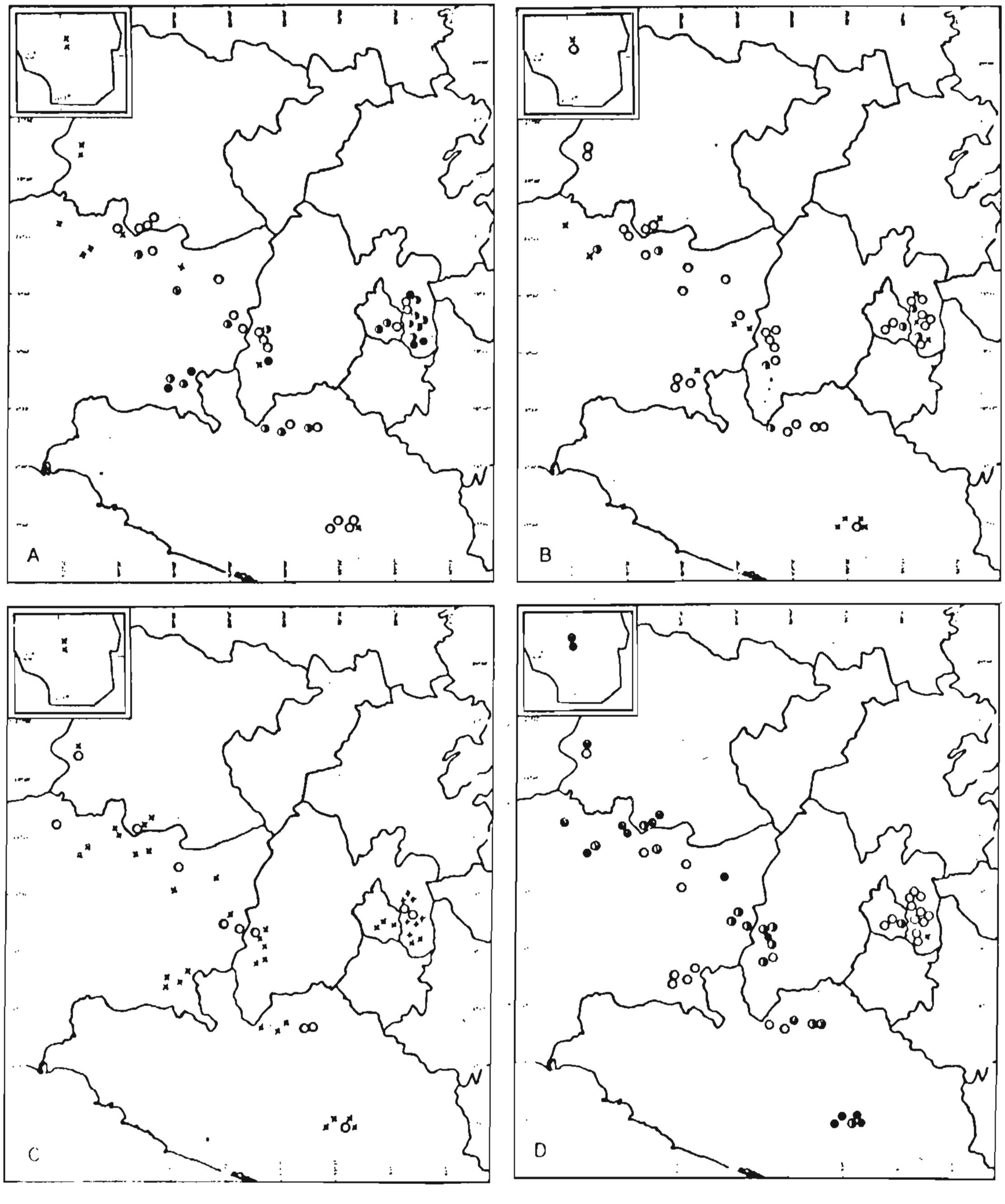

FIGURE 1. Frequency distribution of knobs at the 1S2 position in teosinte collections from Mexico.

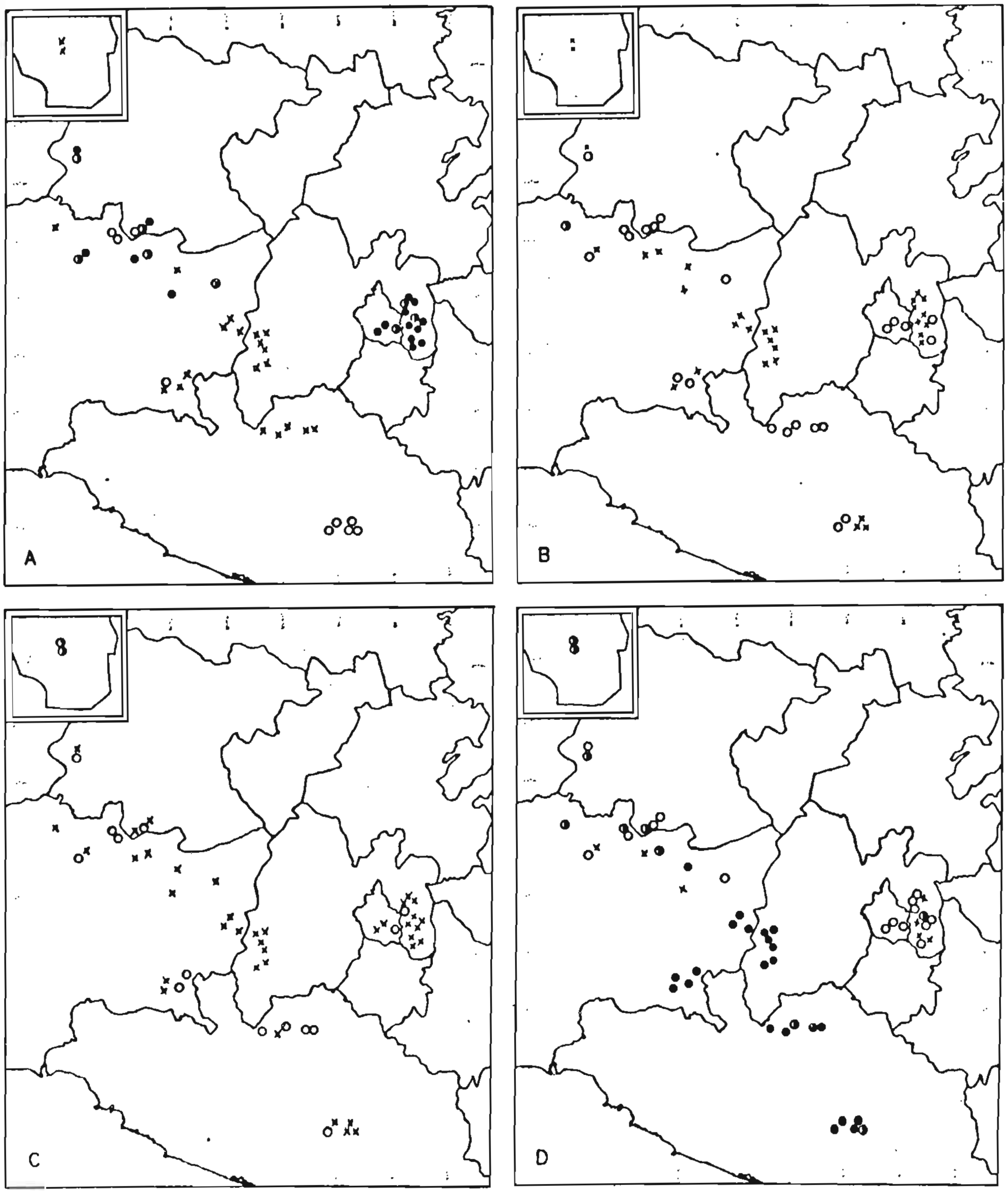

FIGURE 2. Frequency distribution of knobs at the $1L_1$ position in teosinte collections from Mexico.

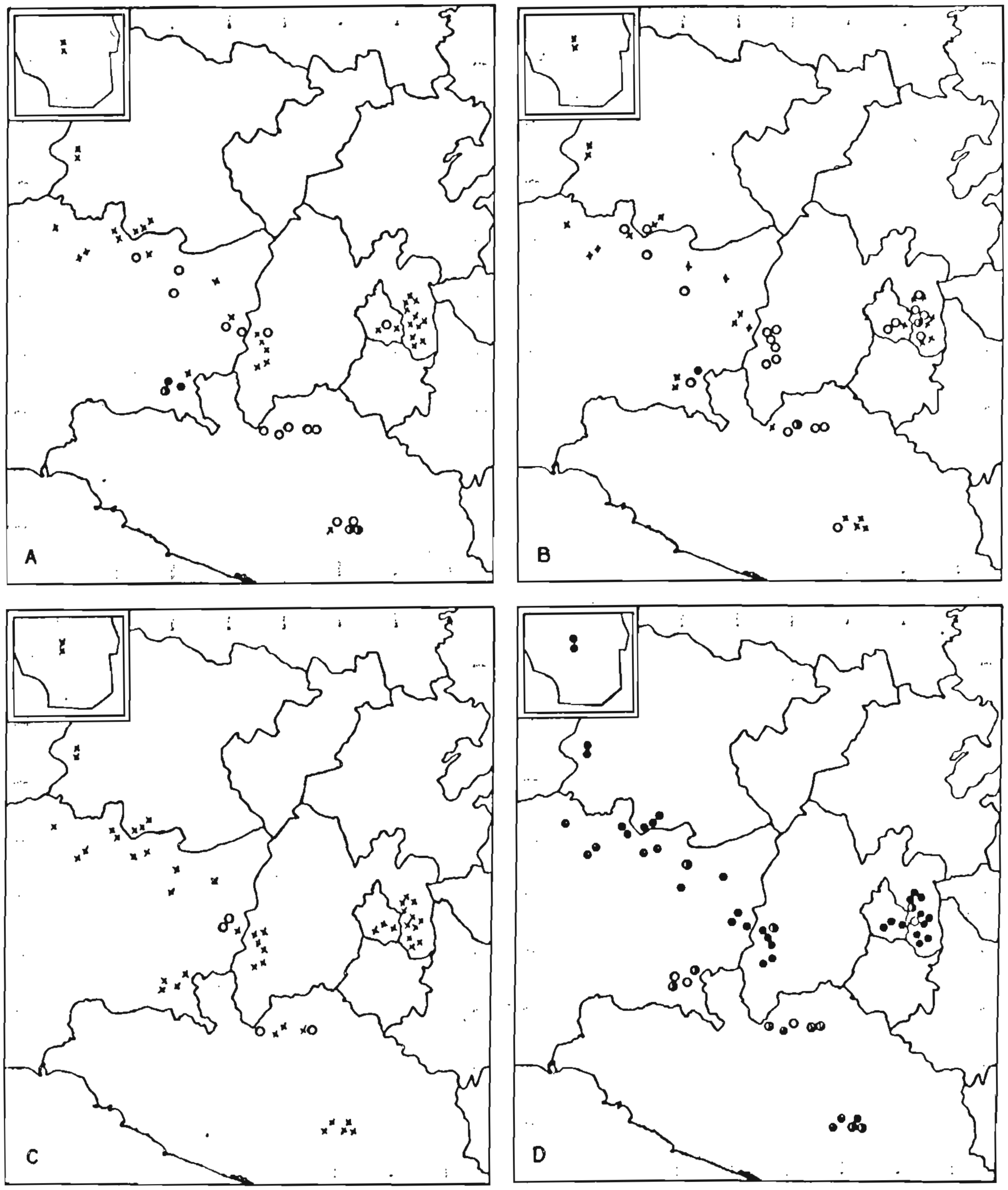

FIGURE 3. Frequency distribution of knobs at the $3S_1$ position in teosinte collections from Mexico.

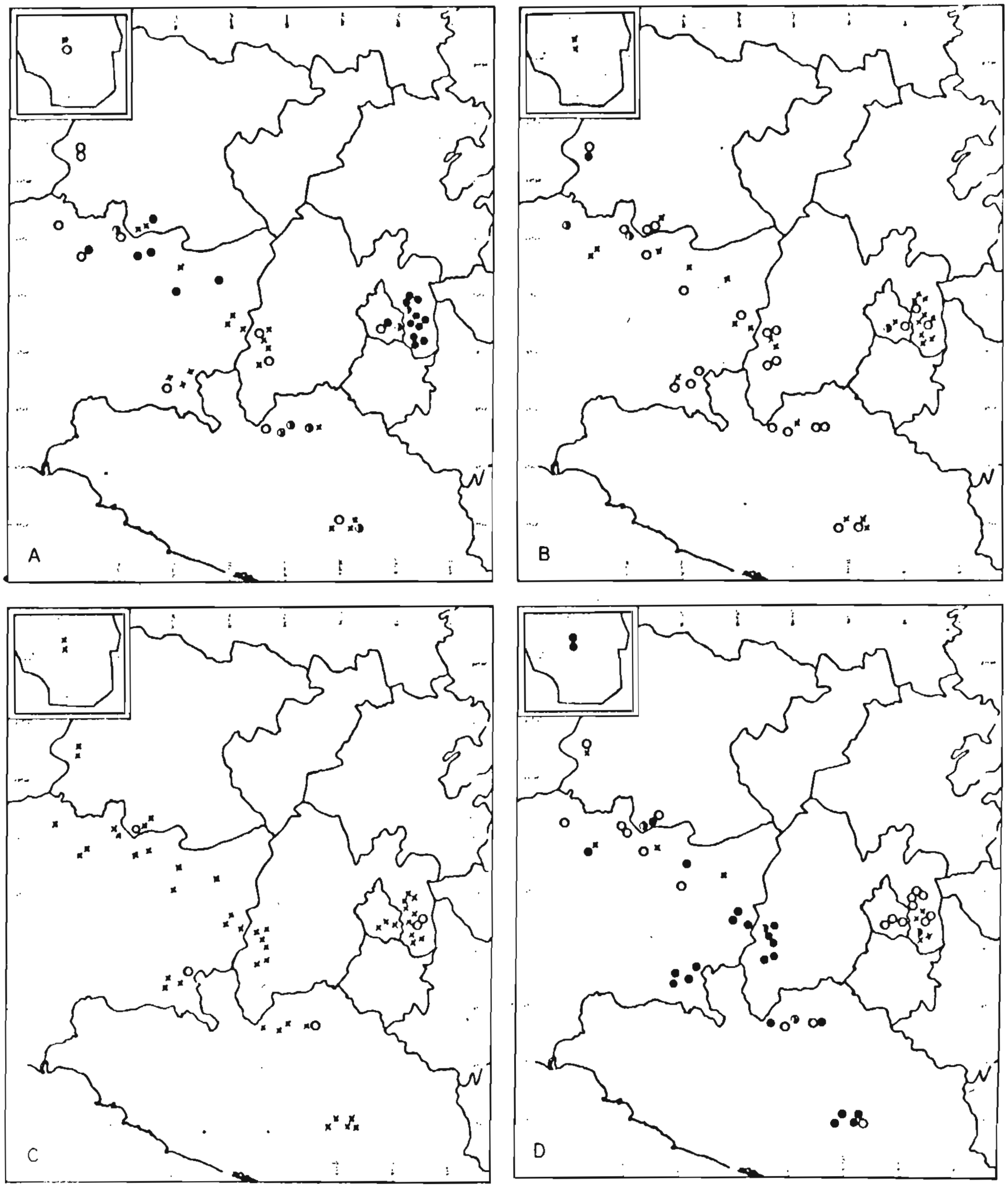

FIGURE 4. Frequency distribution of knobs at the $3L_1$ position in teosinte collections from Mexico.

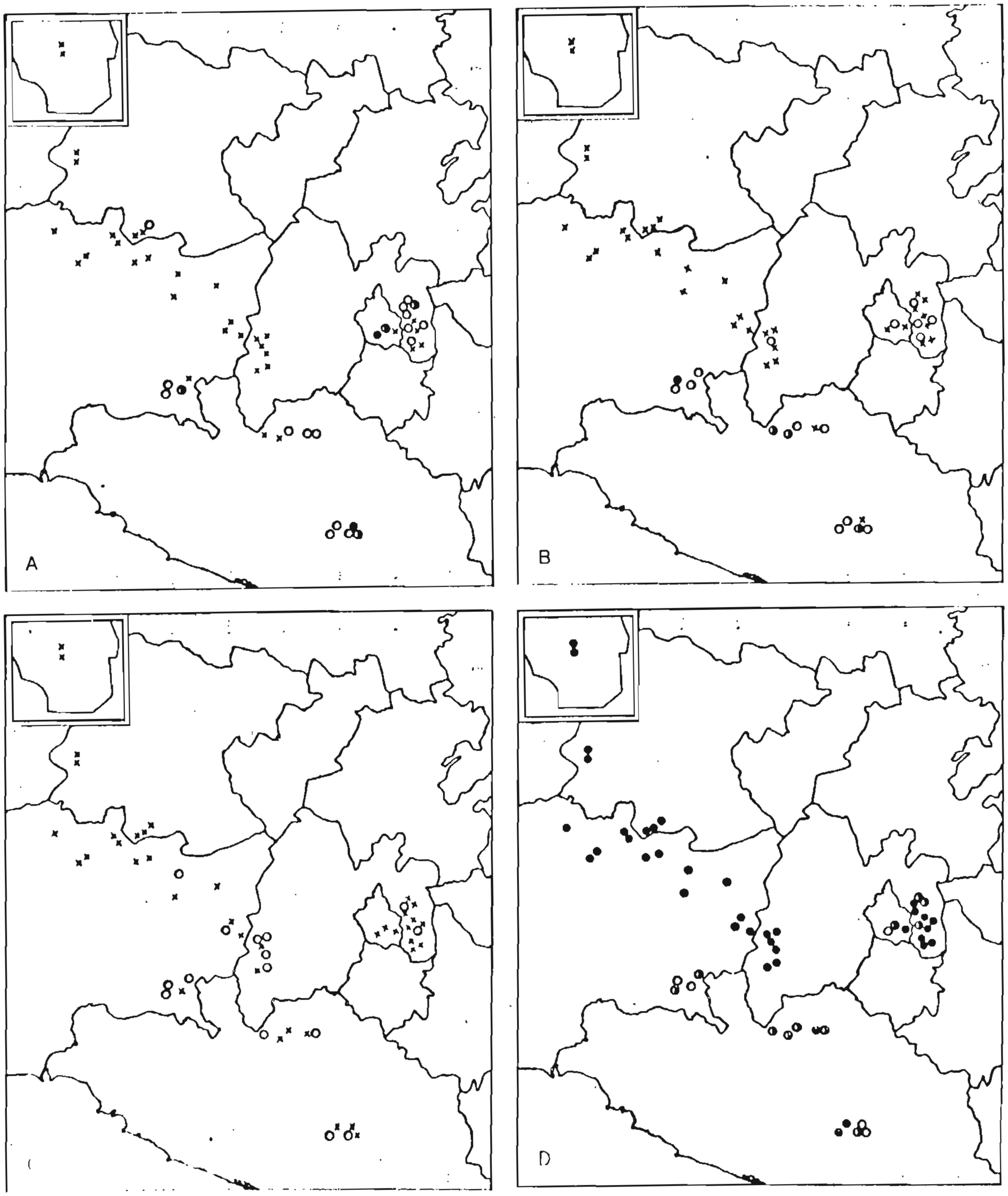

FIGURE 5. Frequency distribution of knobs at the $4S_2$ position in teosinte collections from Mexico.

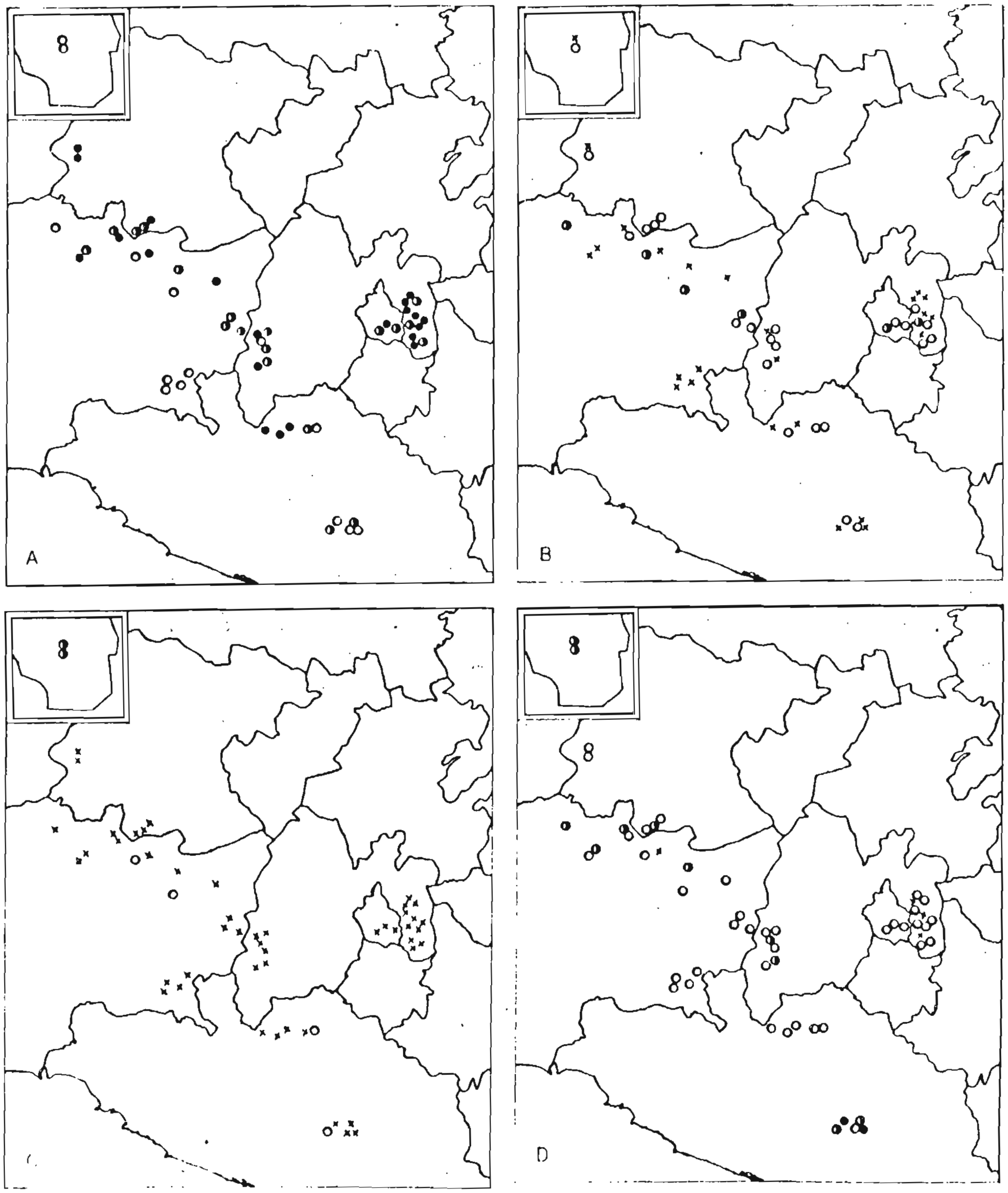

FIGURE 6. Frequency distribution of knobs at the $4L_1$ position in teosinte collections from Mexico.

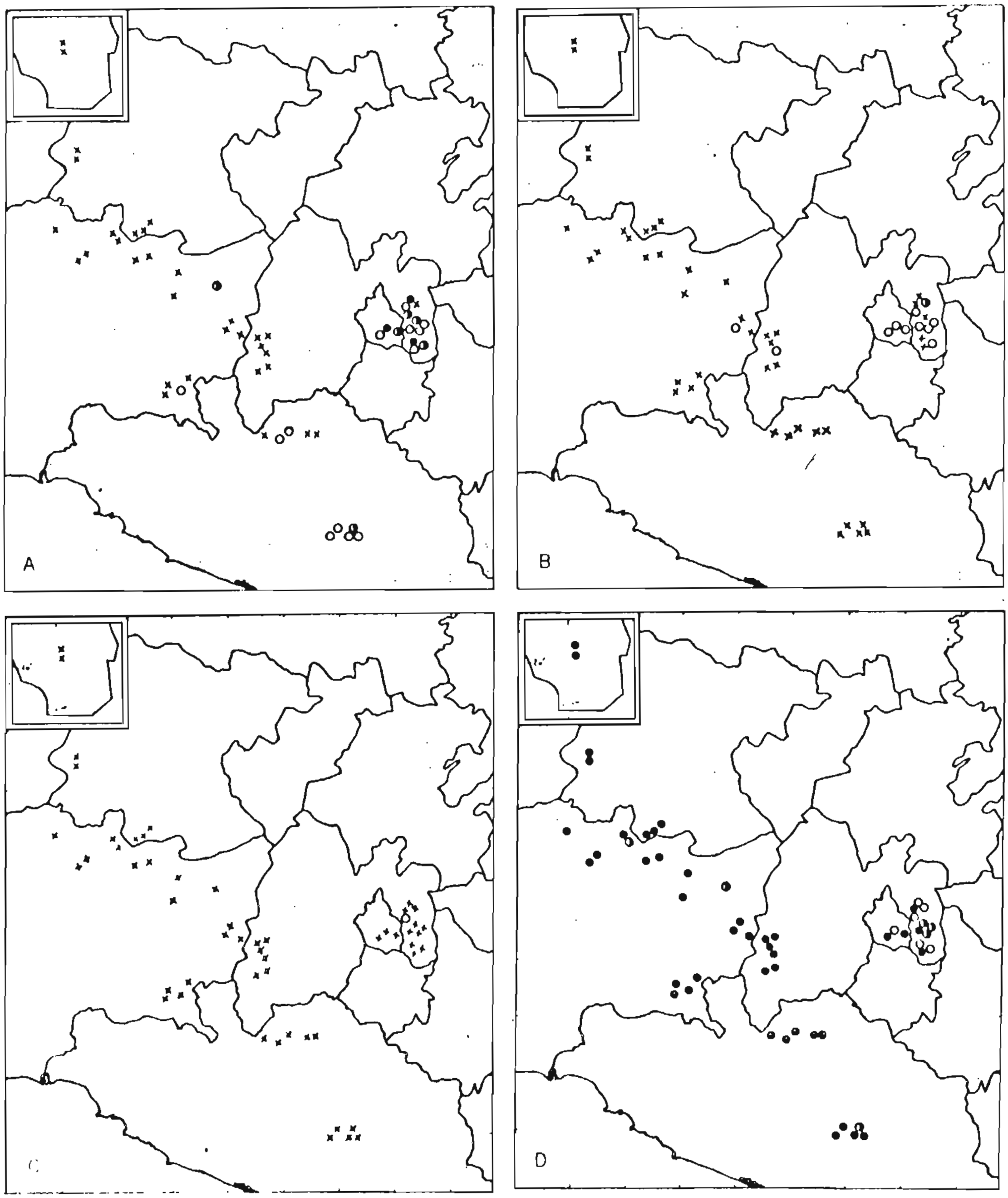

FIGURE 7. Frequency distribution of knobs at the $5S_1$ position in teosinte collections from Mexico.

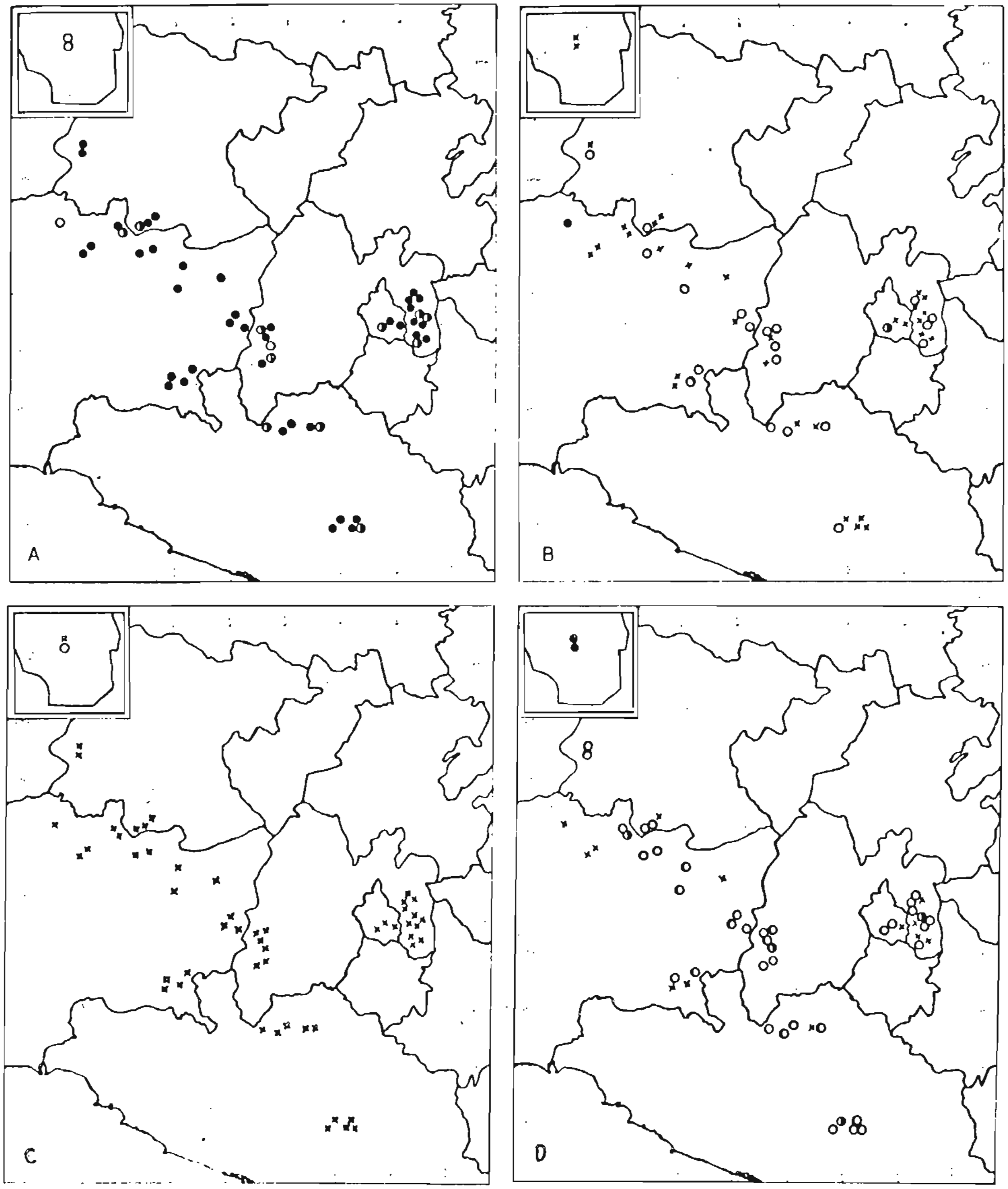

FIGURE 8. Frequency distribution of knobs at the $5L_1$ position in teosinte collections from Mexico.

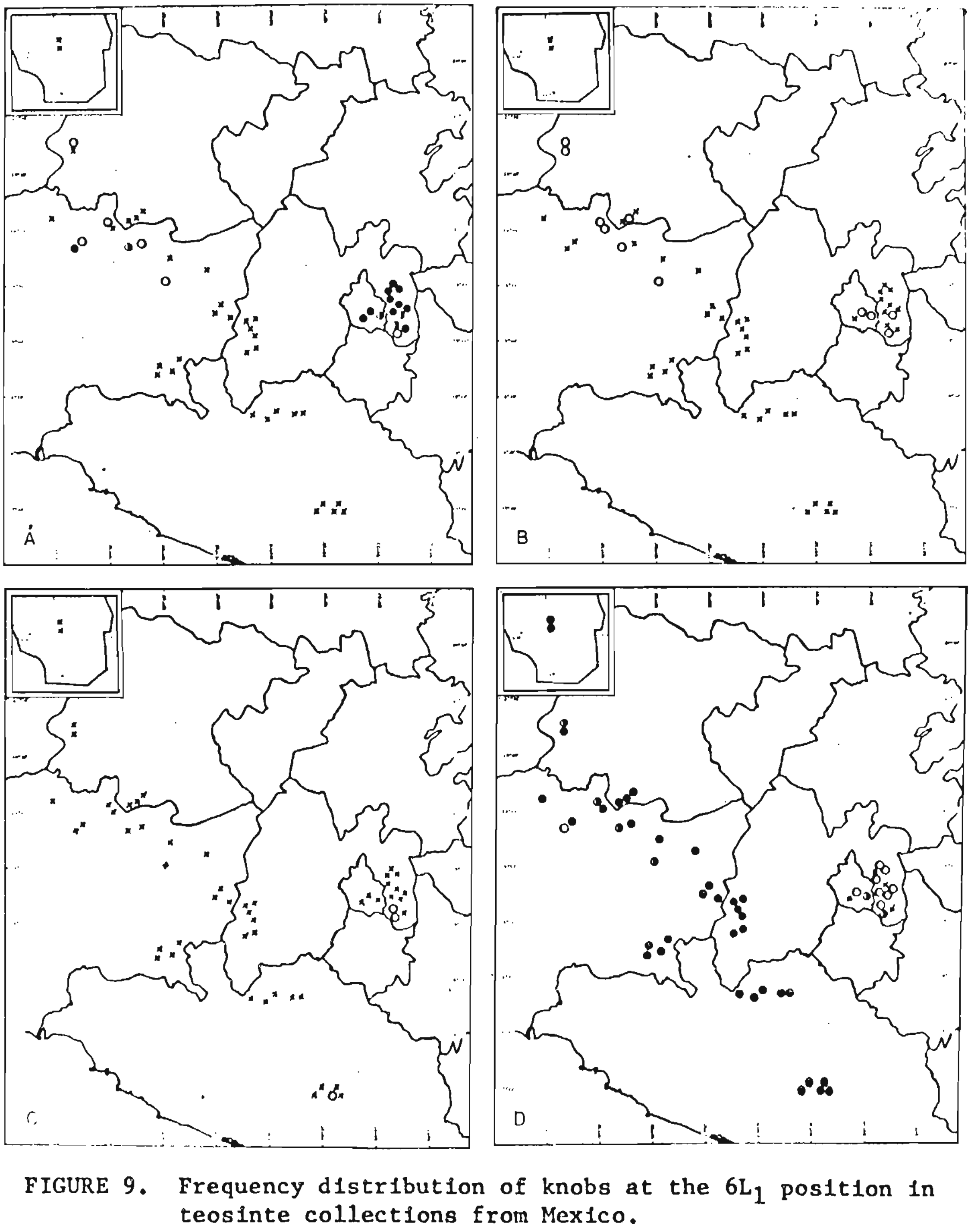

FIGURE 9. Frequency distribution of knobs at the $6L_1$ position in teosinte collections from Mexico.

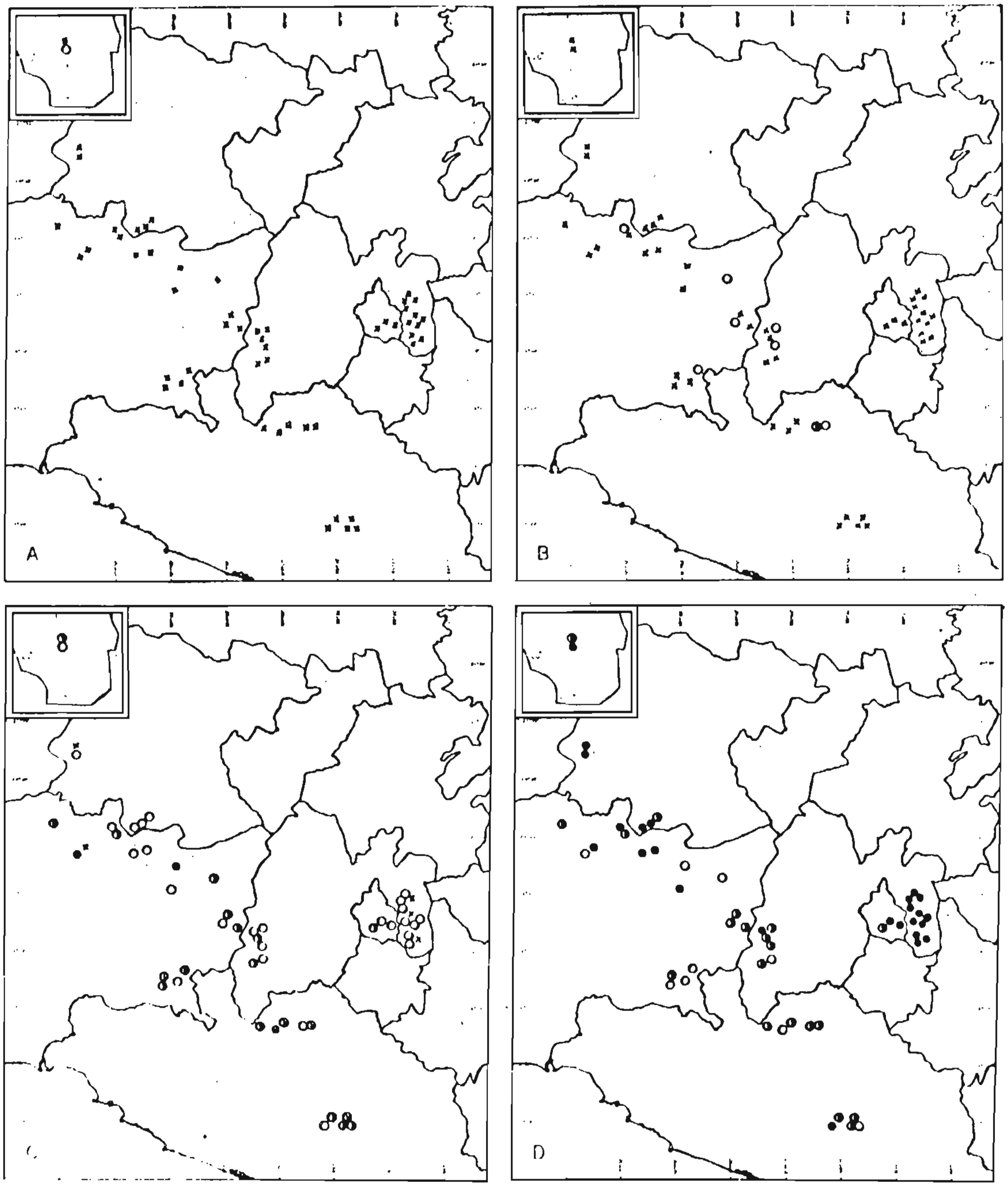

FIGURE 10. Frequency distribution of knobs at the $6L_2$ position in teosinte collections from Mexico.

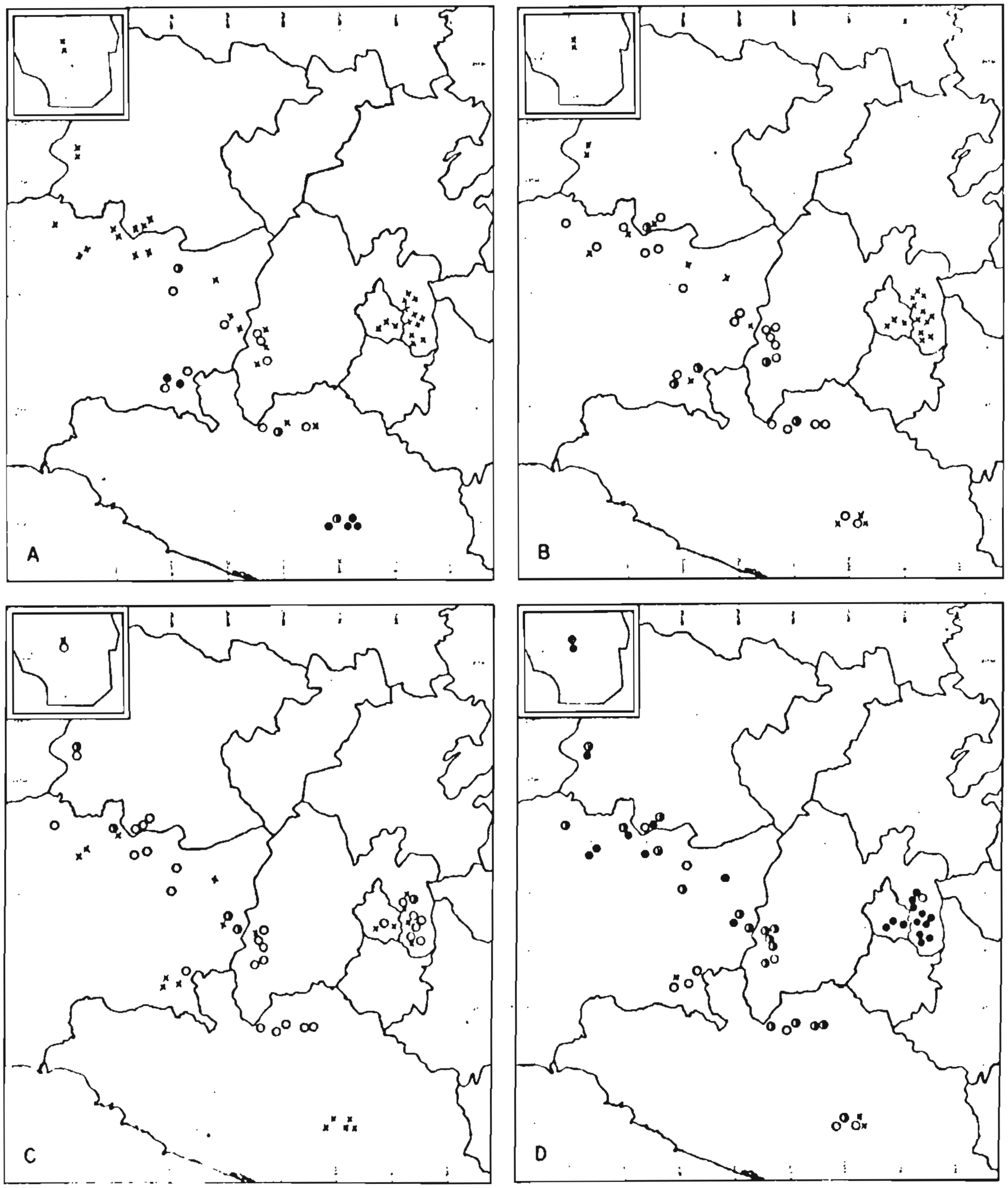

FIGURE 11. Frequency distribution of knobs at the $6L_3$ position in teosinte collections from Mexico.

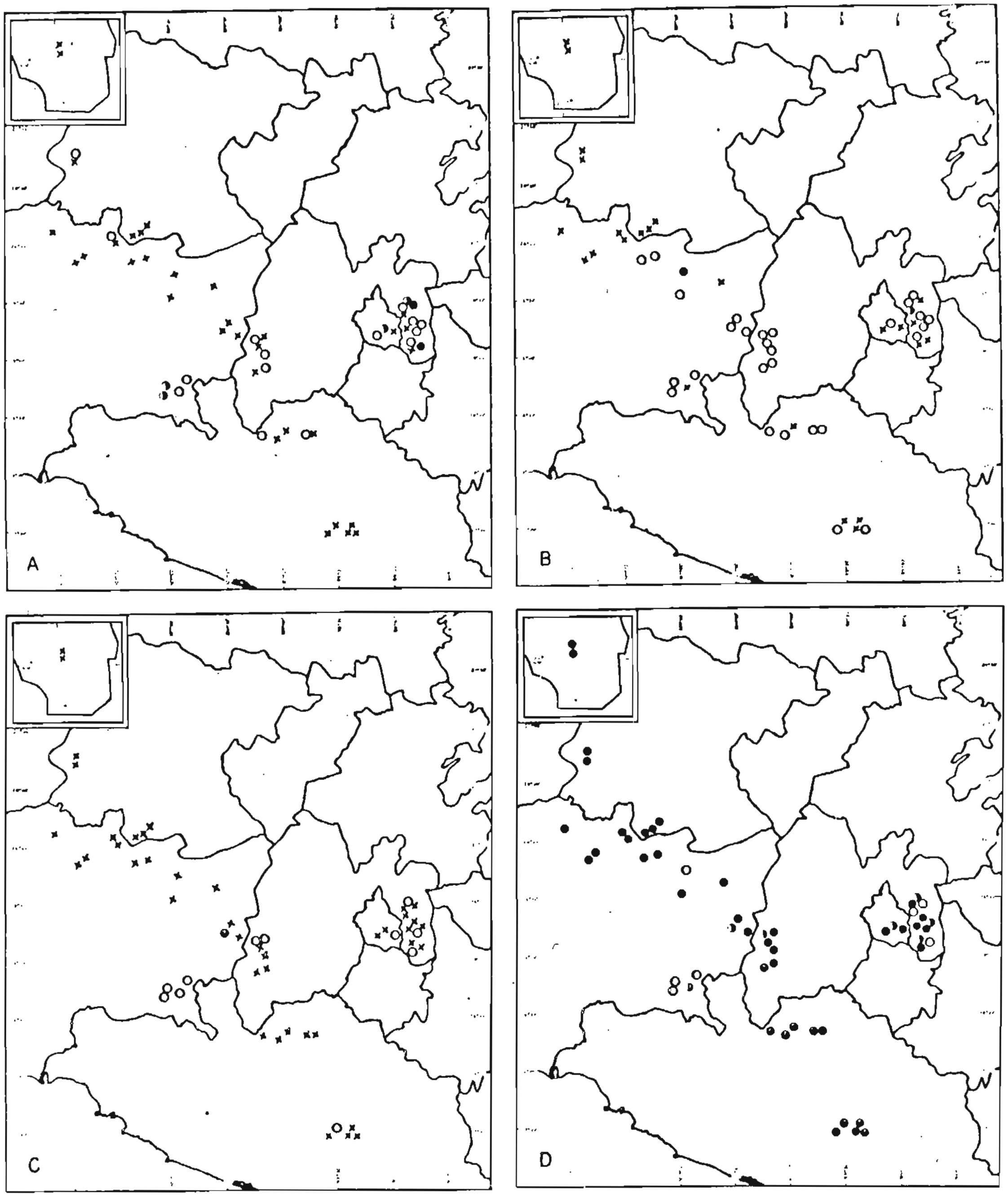

FIGURE 12. Frequency distribution of knobs at the 7S position in teosinte collections from Mexico.

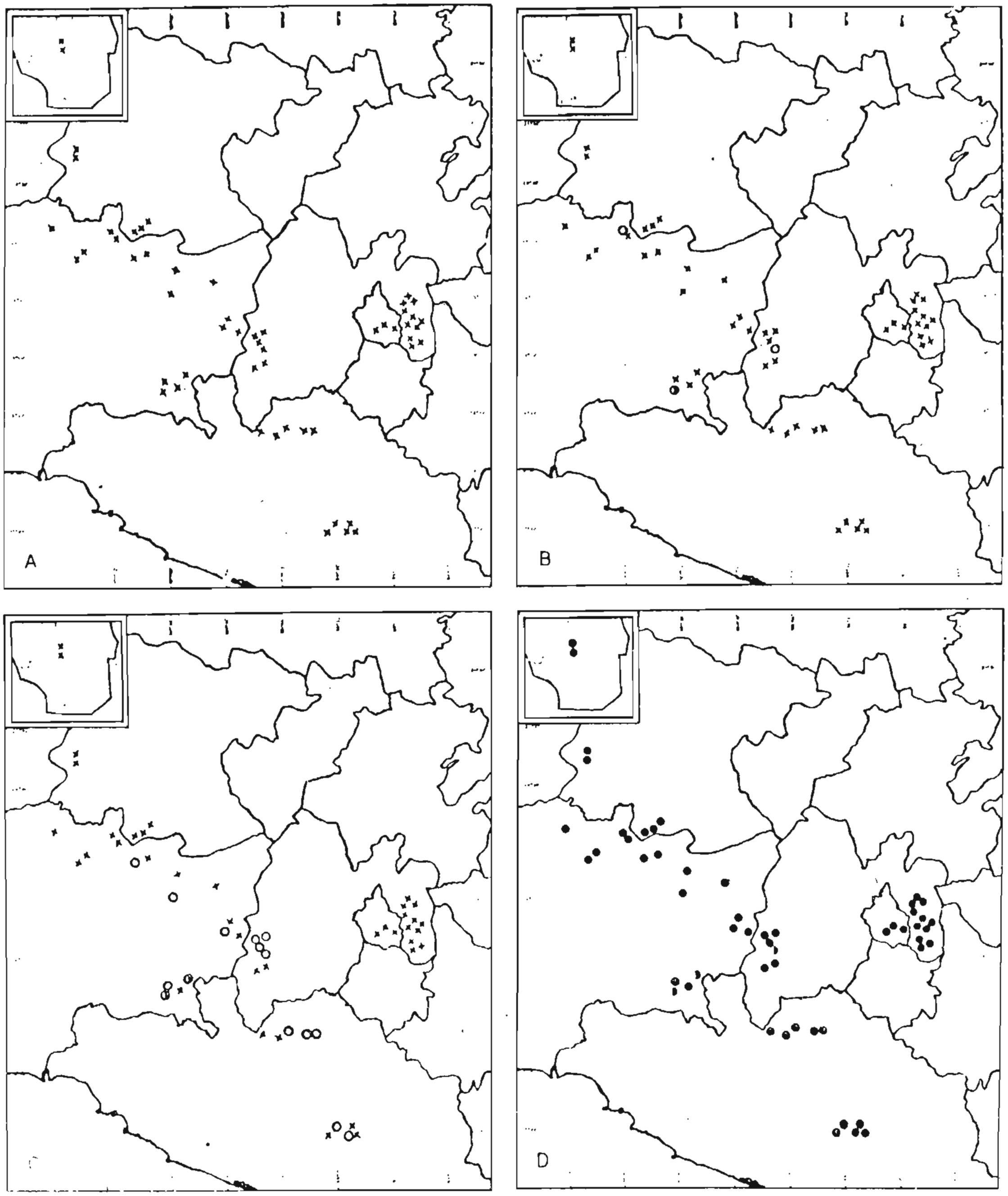

FIGURE 13. Frequency distribution of knobs at the 8S position in teosinte collections from Mexico.

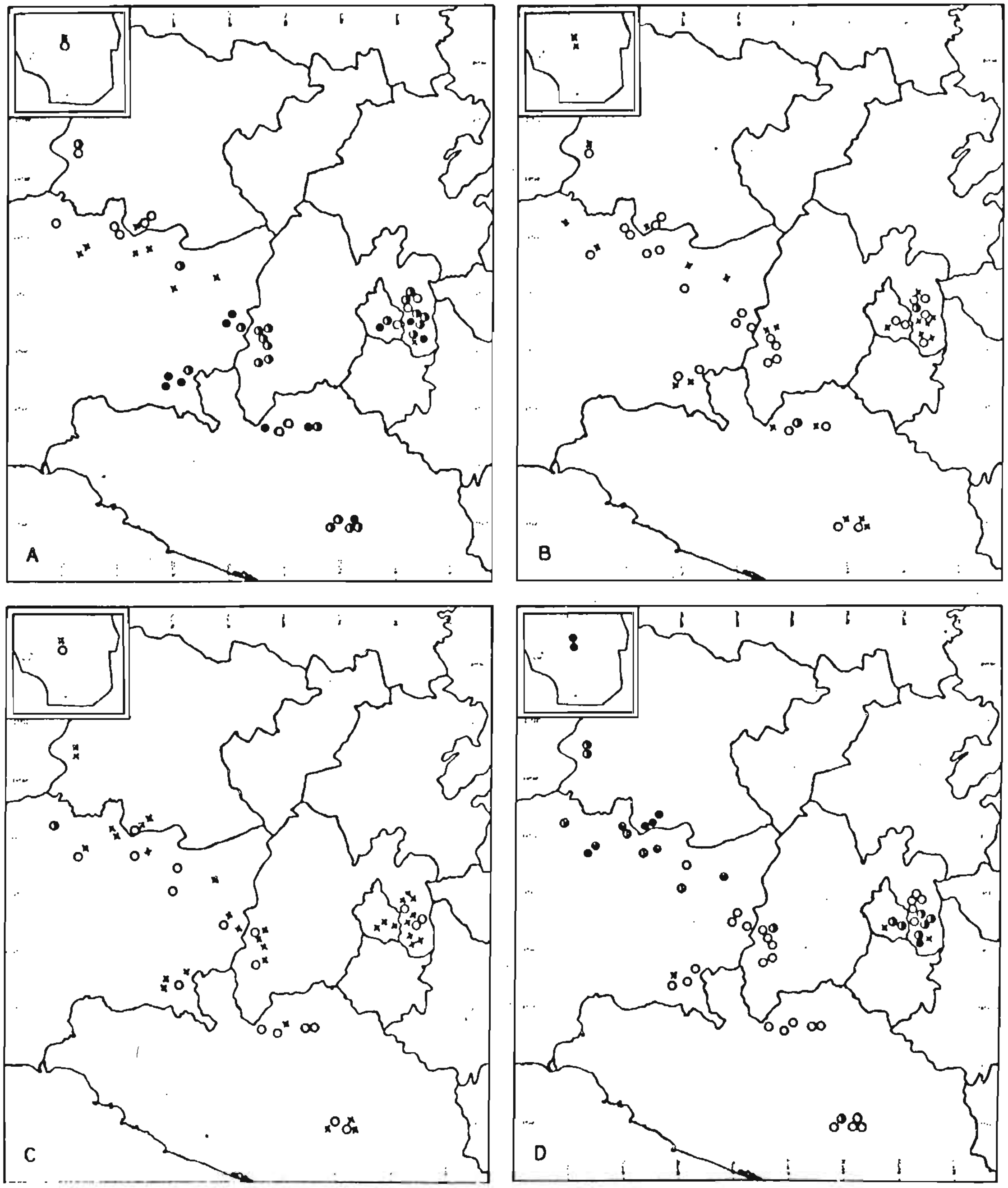

FIGURE 14. Frequency distribution of knobs at the 9S position in teosinte collections from Mexico.

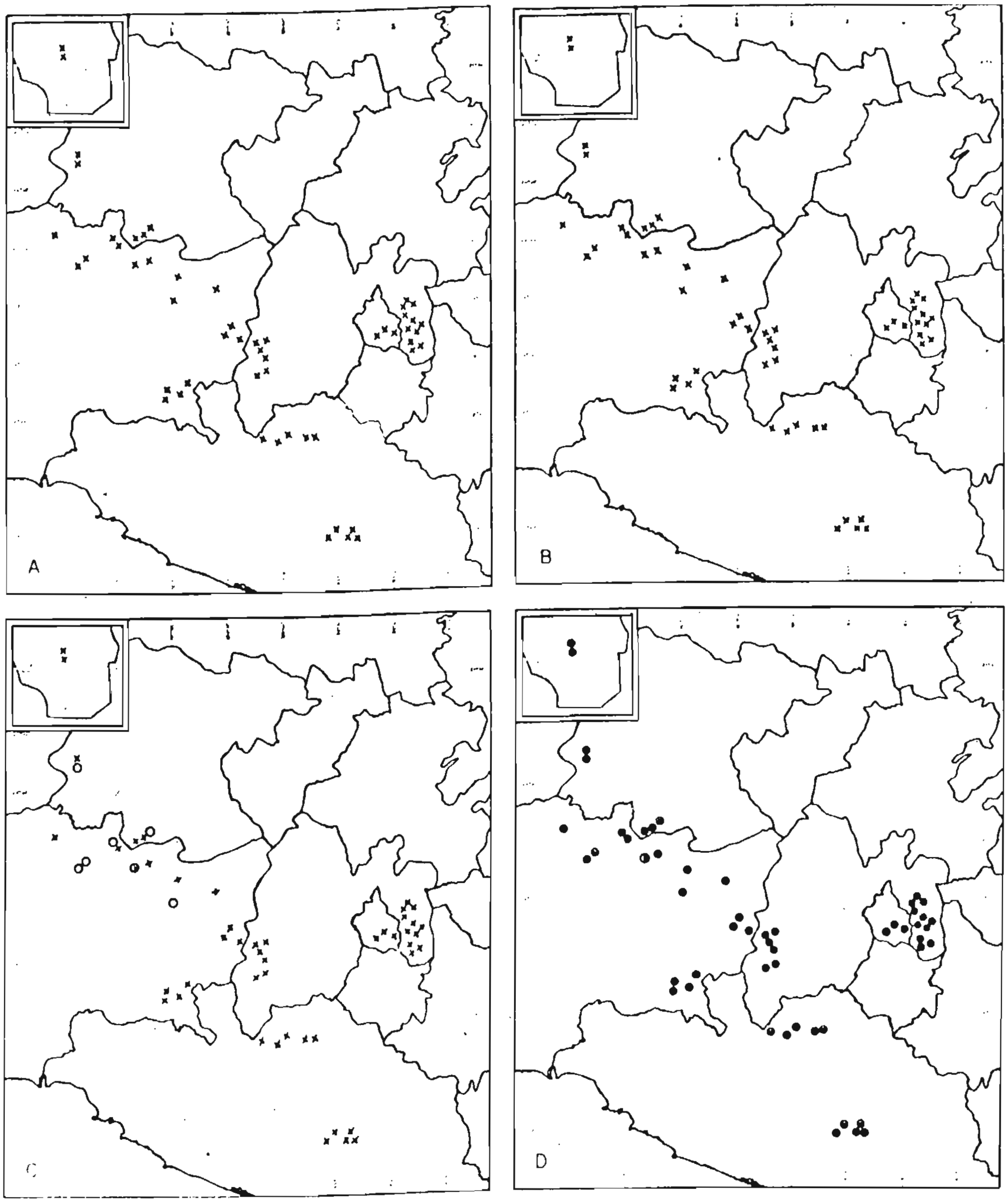

FIGURE 15. Frequency distribution of knobs at the $9L_1$ position in teosinte collections from Mexico.

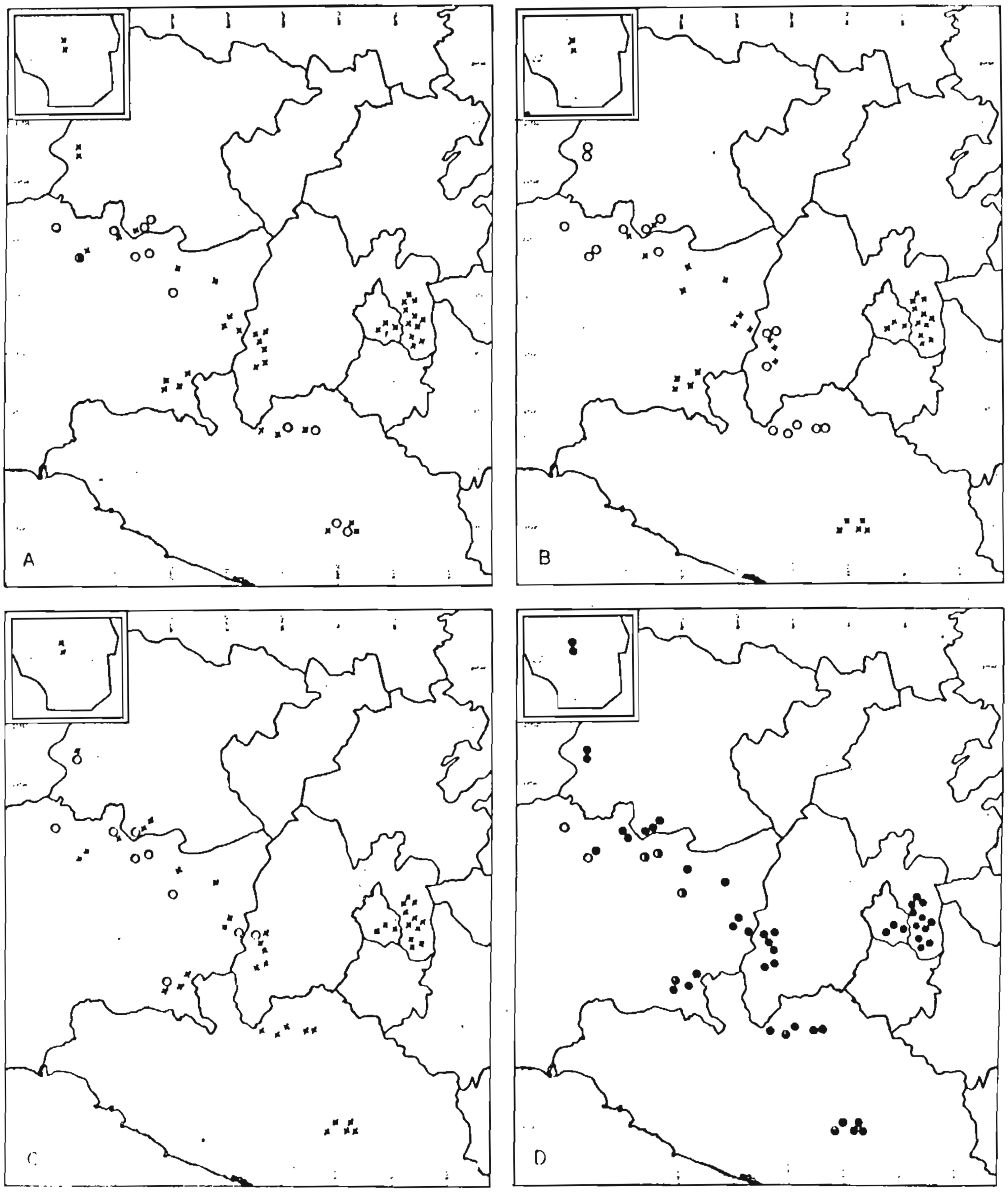

FIGURE 16. Frequency distribution of knobs at the $9L_2$ position in teosinte collections from Mexico.

FIGURES 17 to 29. Geographical distribution of the relative frequencies of the several knob sizes [large, medium, small and knobless] found at different knob positions in collections of maize from central Mexico.

In each figure, the maps illustrate the distribution of: A. large knobs; B. medium knobs; C. small knobs; and D. knobless. Each circle represents a single collection. Black circles represent high frequencies [more than 2/3 of the total number of chromosomes of each collection]; half circles represent intermediate frequencies [1/3 to 2/3 of the total chromosomes]; open circles represent low frequencies [less than 1/3 of the total chromosomes]; and the X's represent absence of the particular knob condition that the specific map is considering.

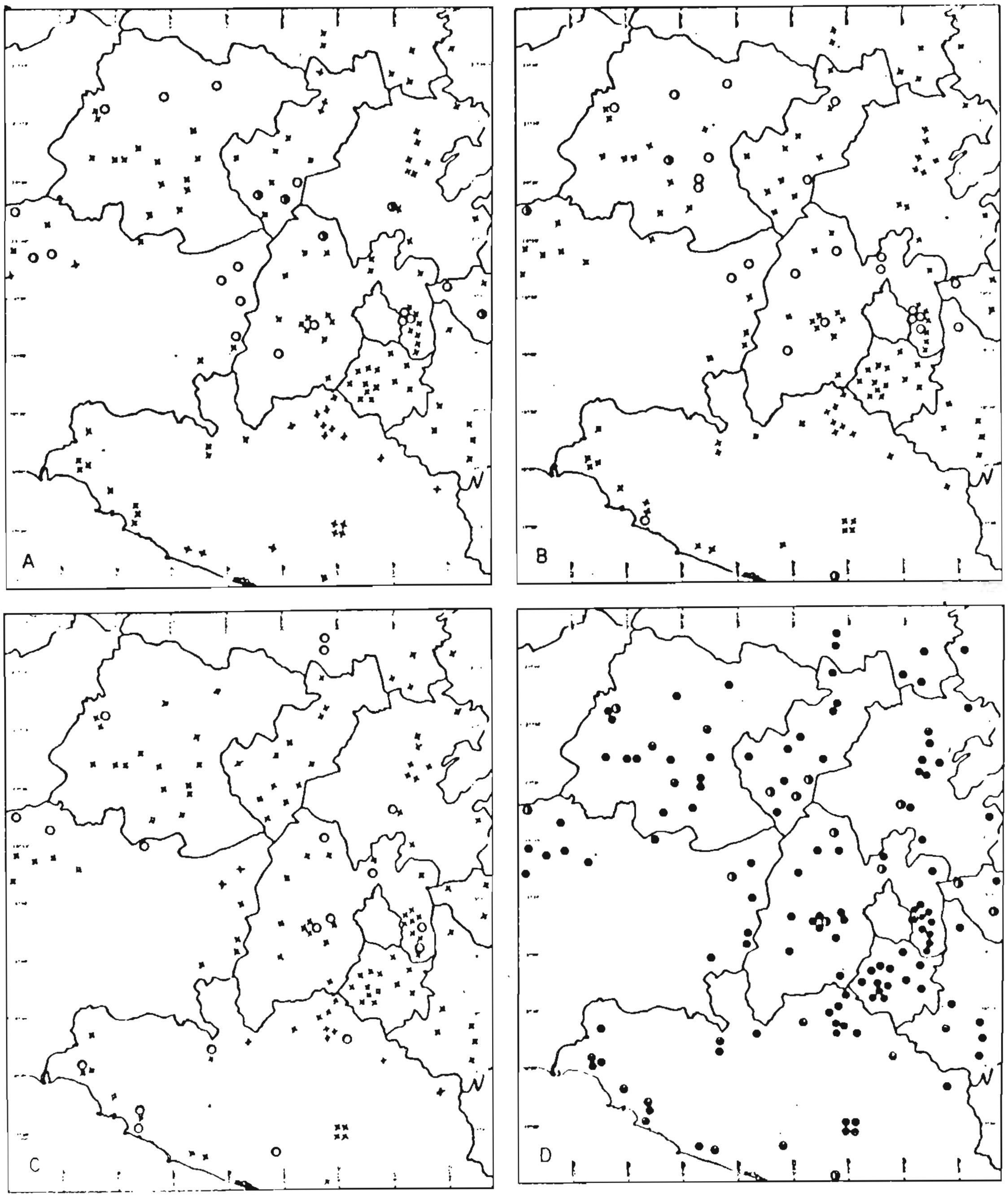

FIGURE 17. Frequency distribution of knobs at the 1L1 position in maize collections from central Mexico.

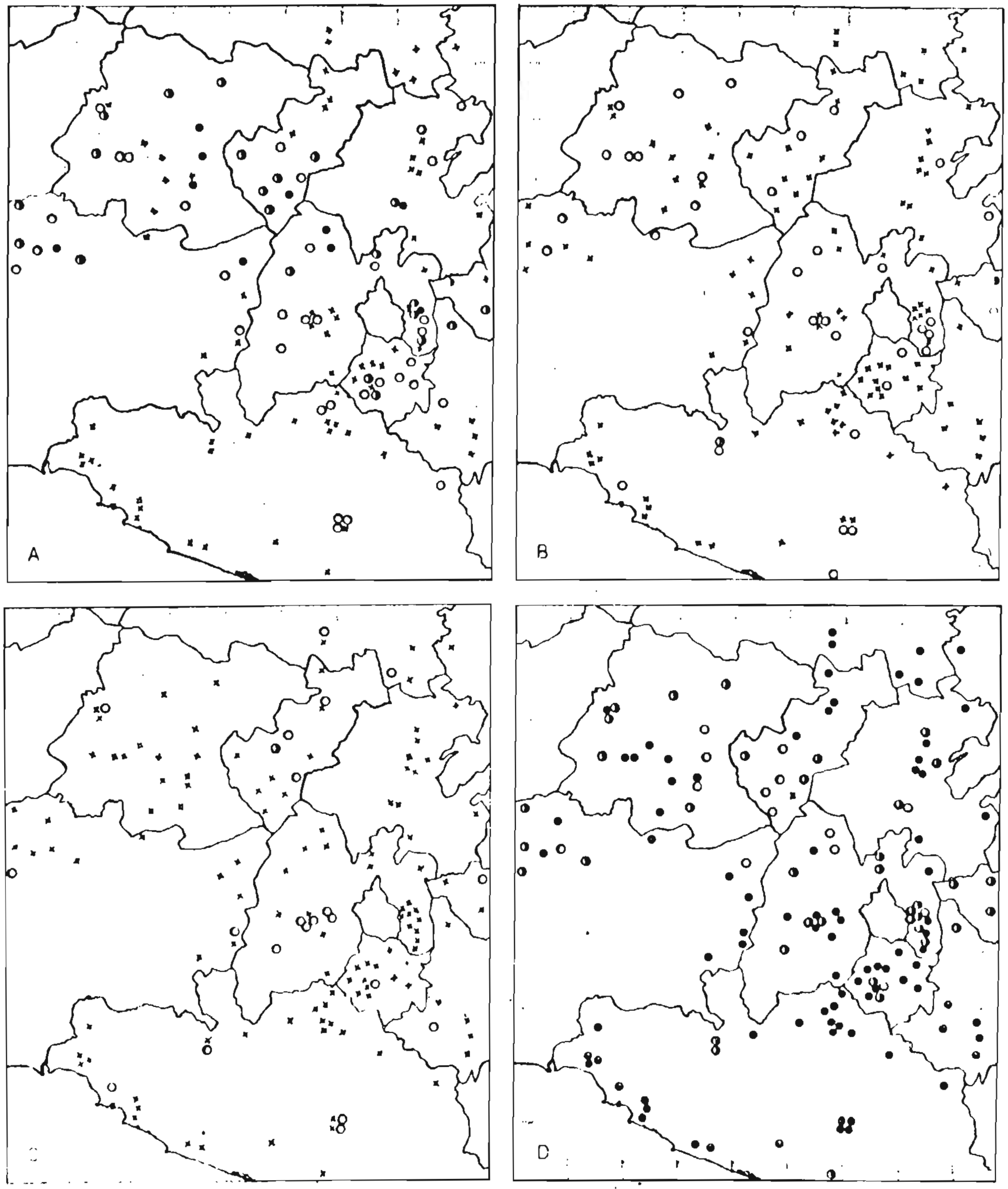

FIGURE 18. Frequency distribution of knobs at the $2S_1$ position in maize collections from central Mexico.

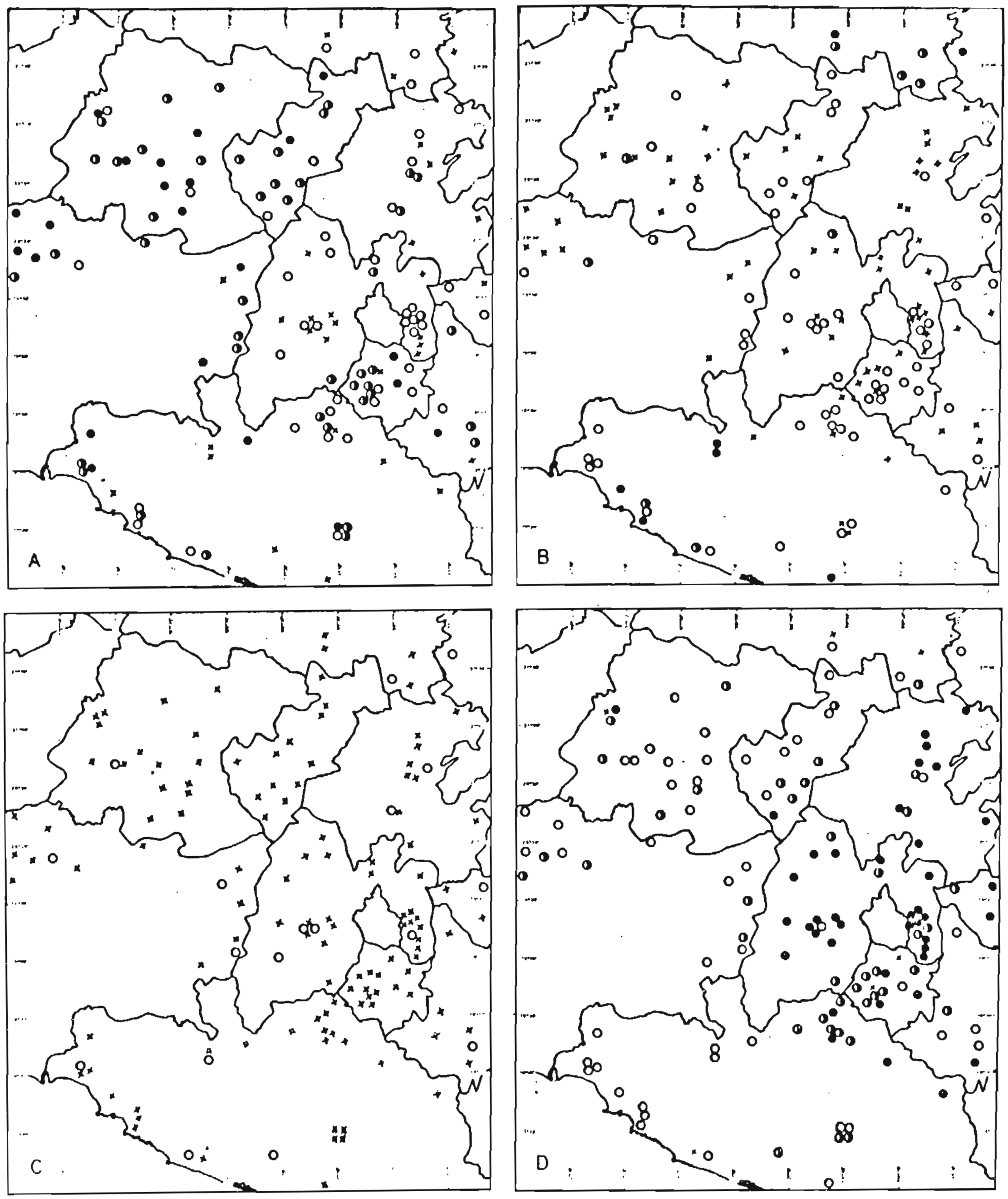

FIGURE 19. Frequency distribution of knobs at the $2L_1$ position in maize collections from central Mexico.

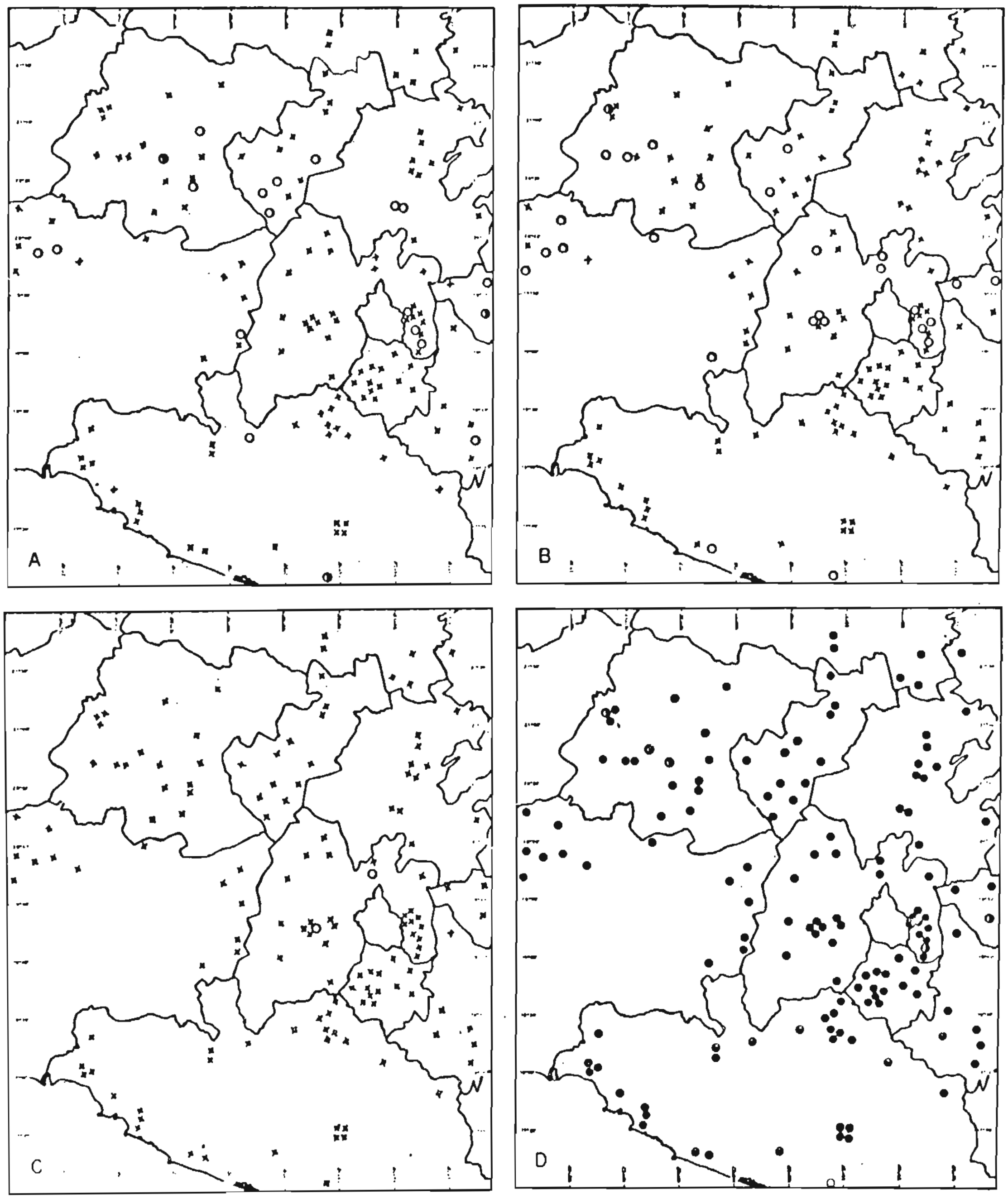

FIGURE 20. Frequency distribution of knobs at the $3S_1$ position in maize collections from central Mexico.

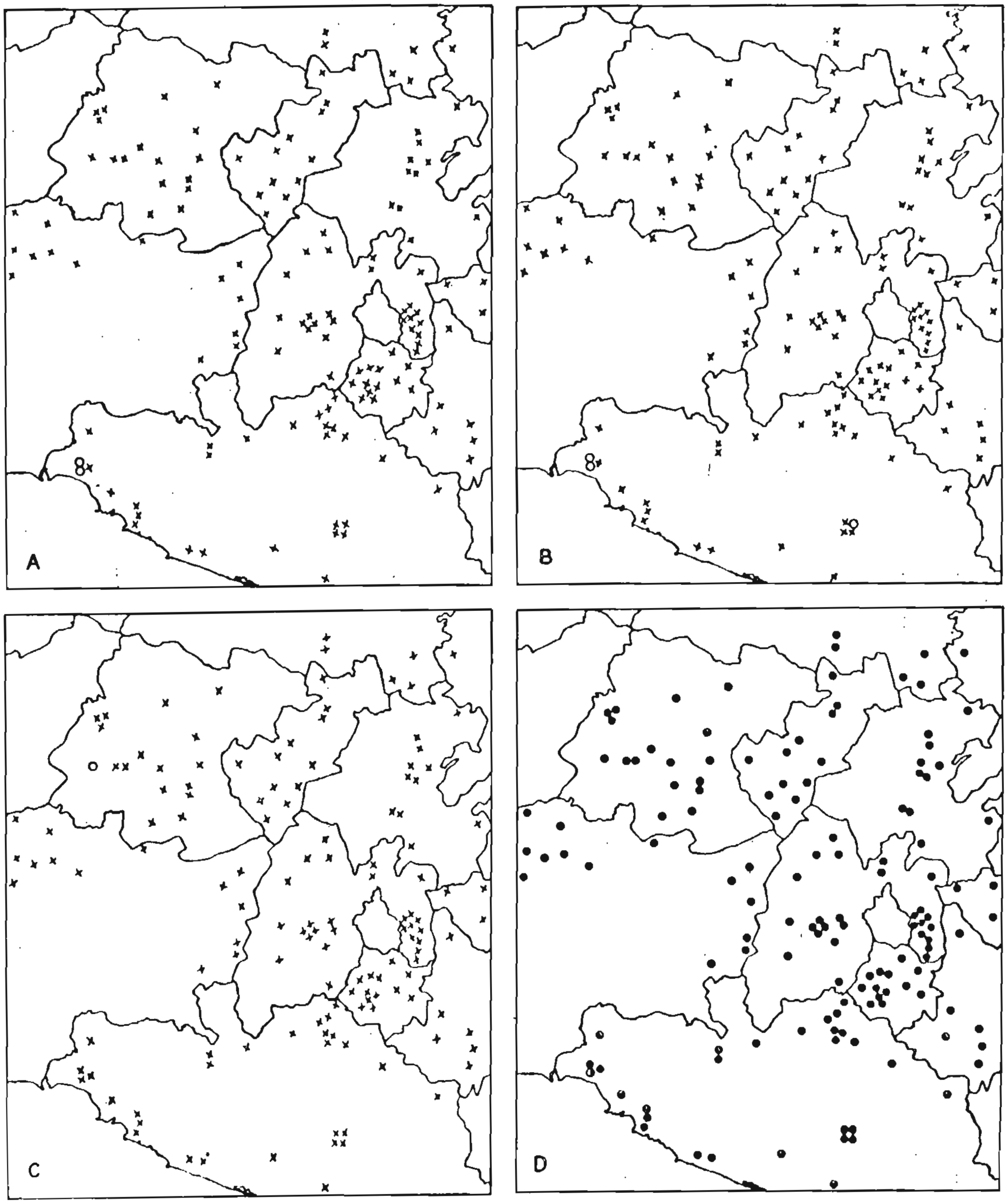

FIGURE 21. Frequency distribution of knobs at the $4S_2$ position in maize collections from central Mexico.

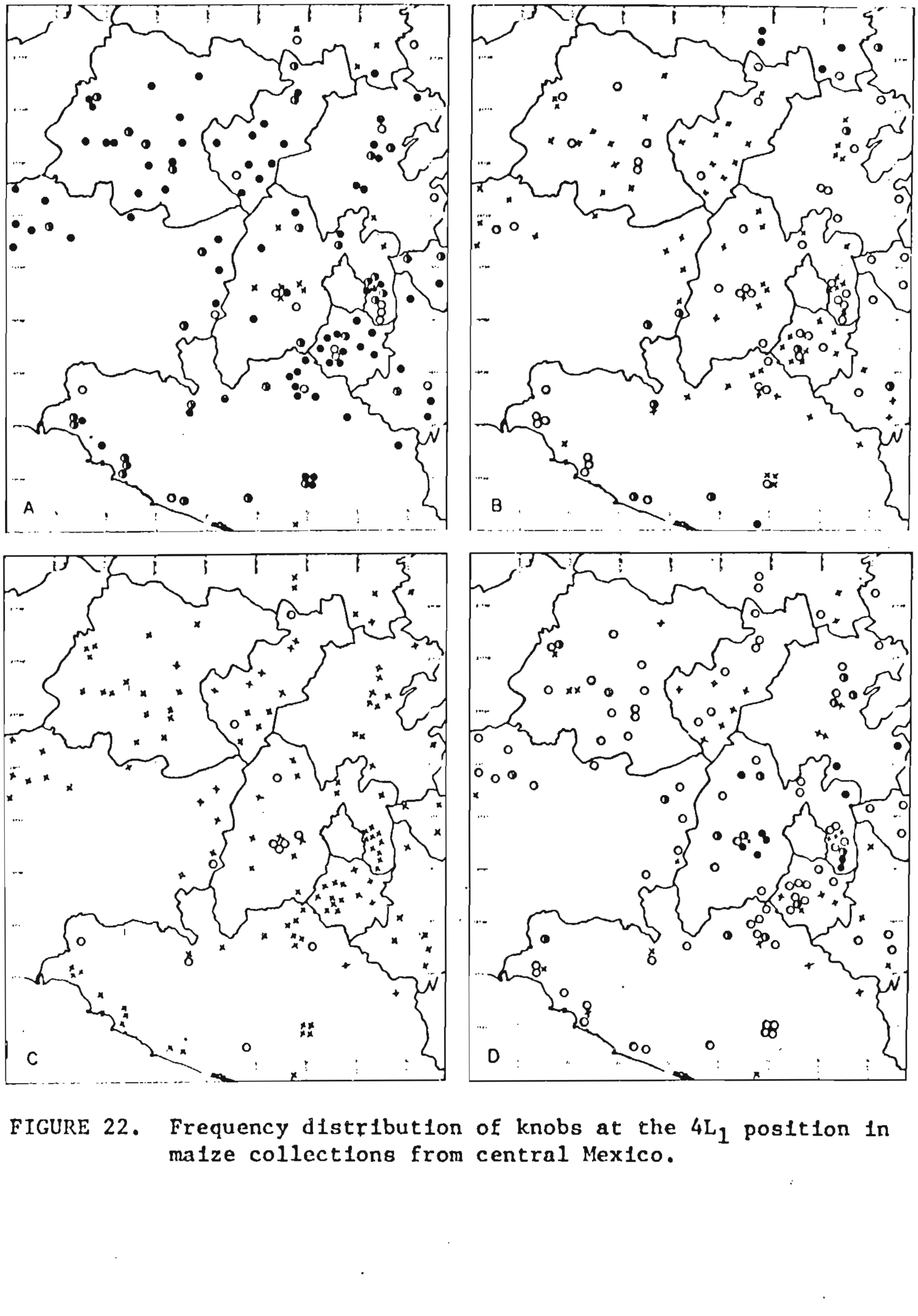

FIGURE 22. Frequency distribution of knobs at the $4L_1$ position in maize collections from central Mexico.

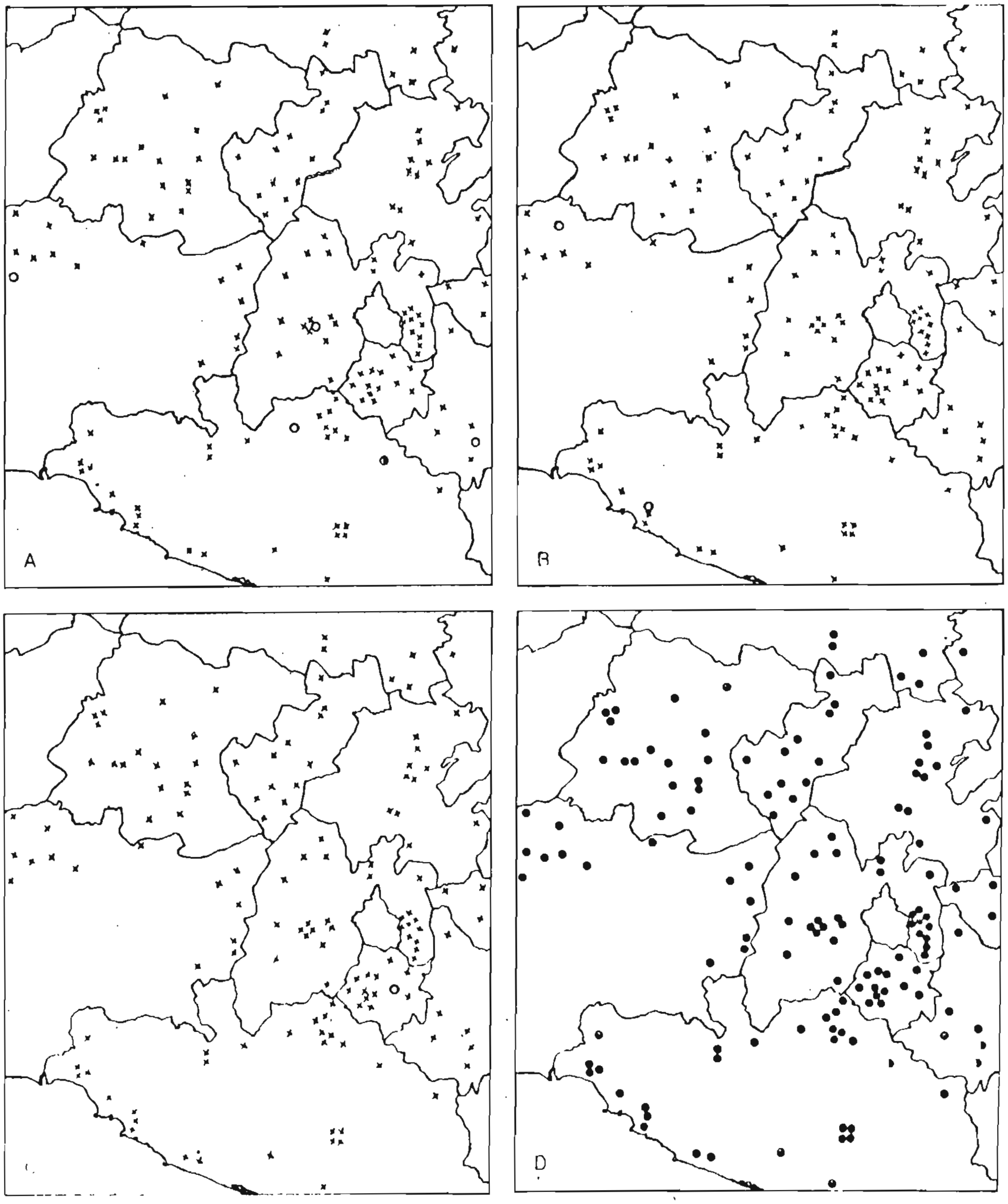

FIGURE 23. Frequency distribution of knobs at the $5S_1$ position in maize collections from central Mexico.

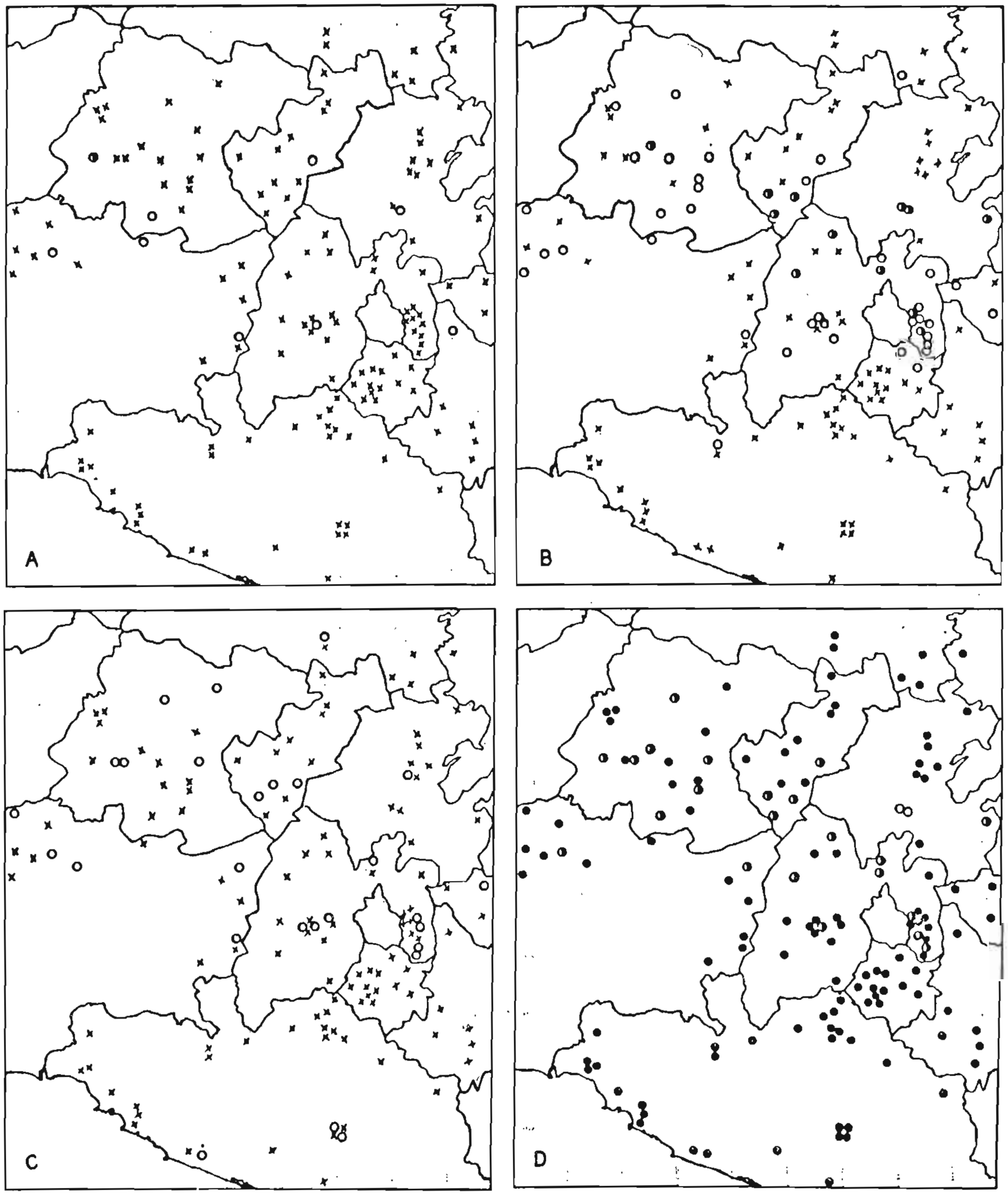

FIGURE 24. Frequency distribution of knobs at the $6L_1$ position in maize collections from central Mexico.

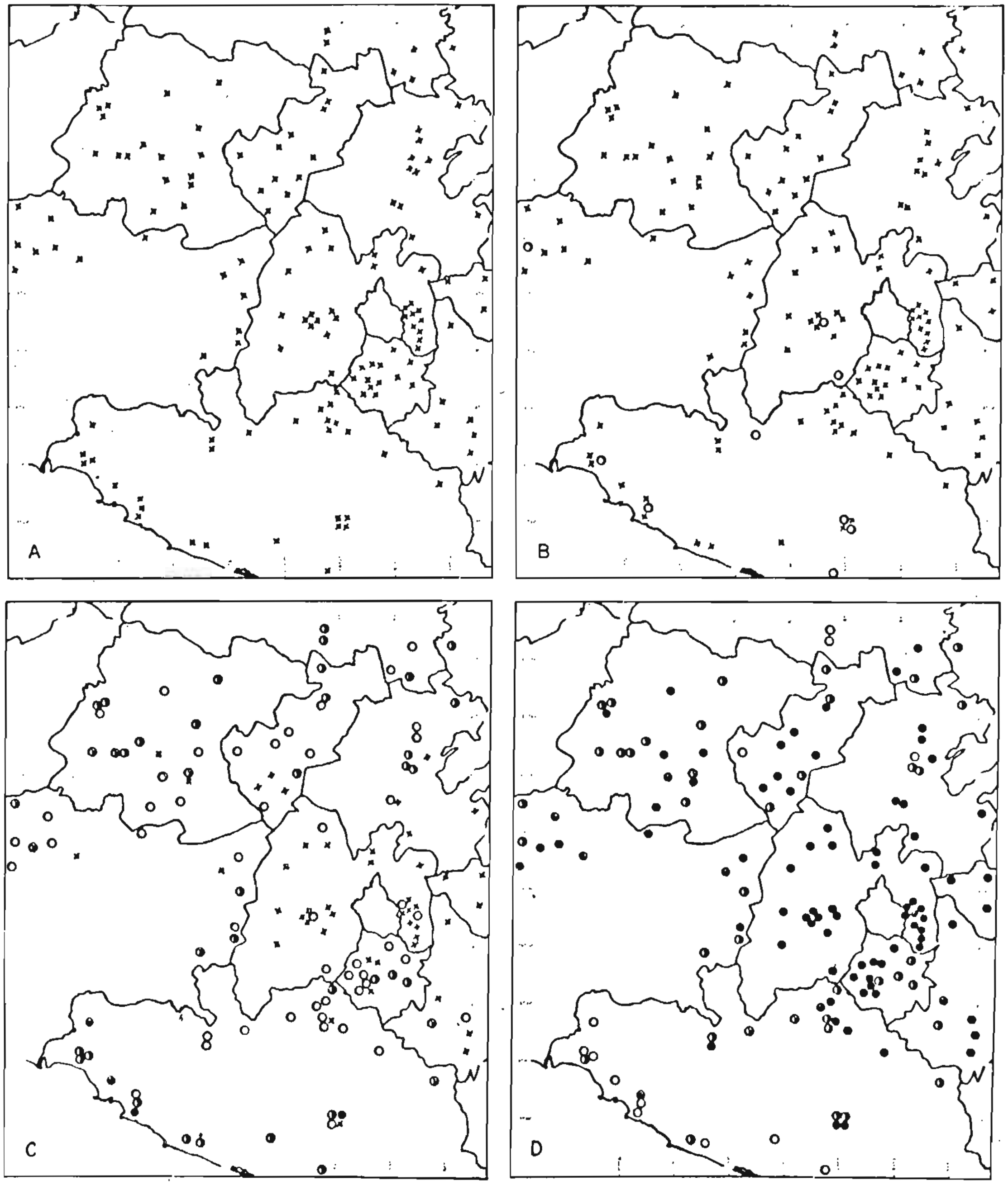

FIGURE 25. Frequency distribution of knobs at the $6L_2$ position in maize collections from central Mexico.

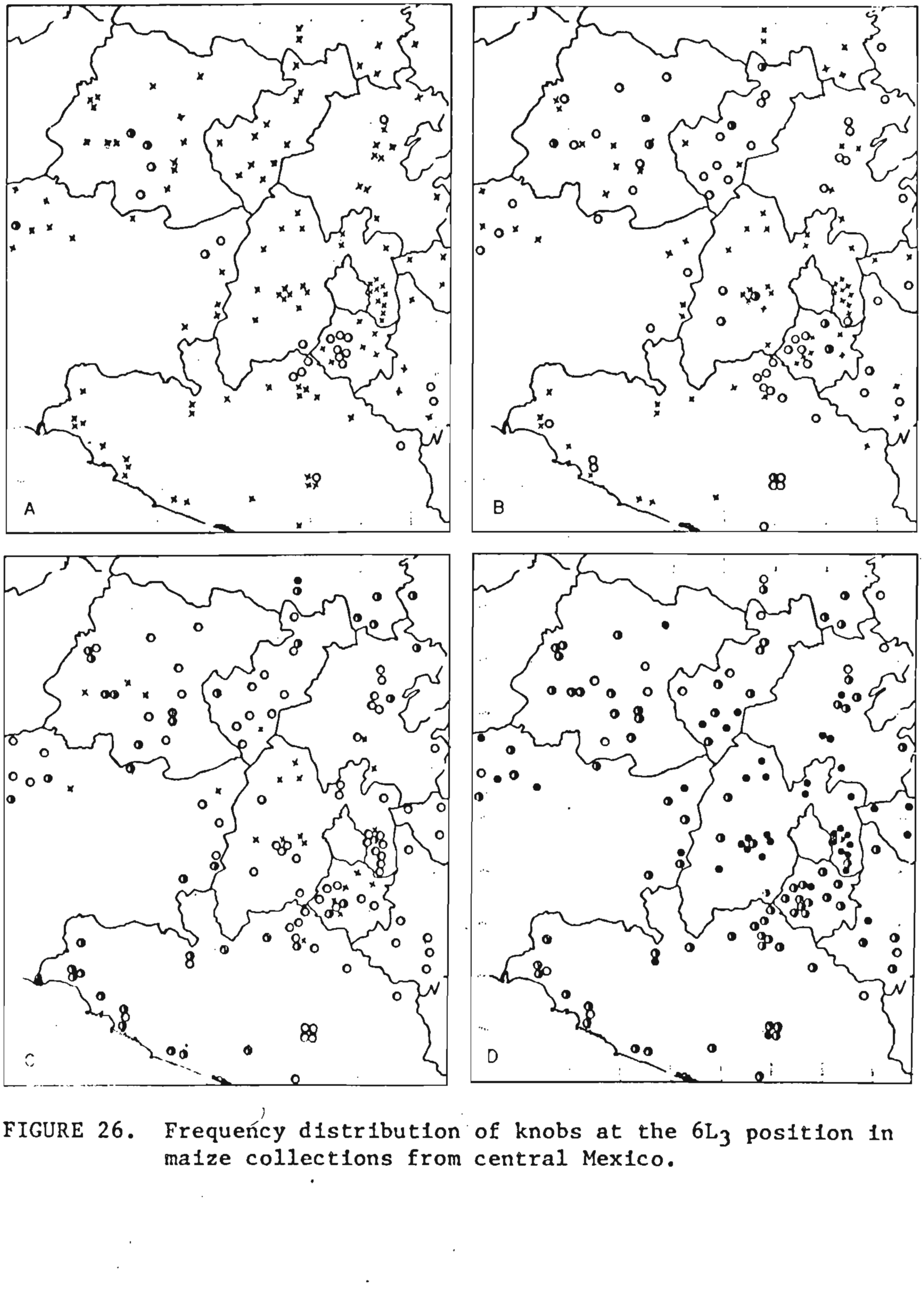

FIGURE 26. Frequency distribution of knobs at the $6L_3$ position in maize collections from central Mexico.

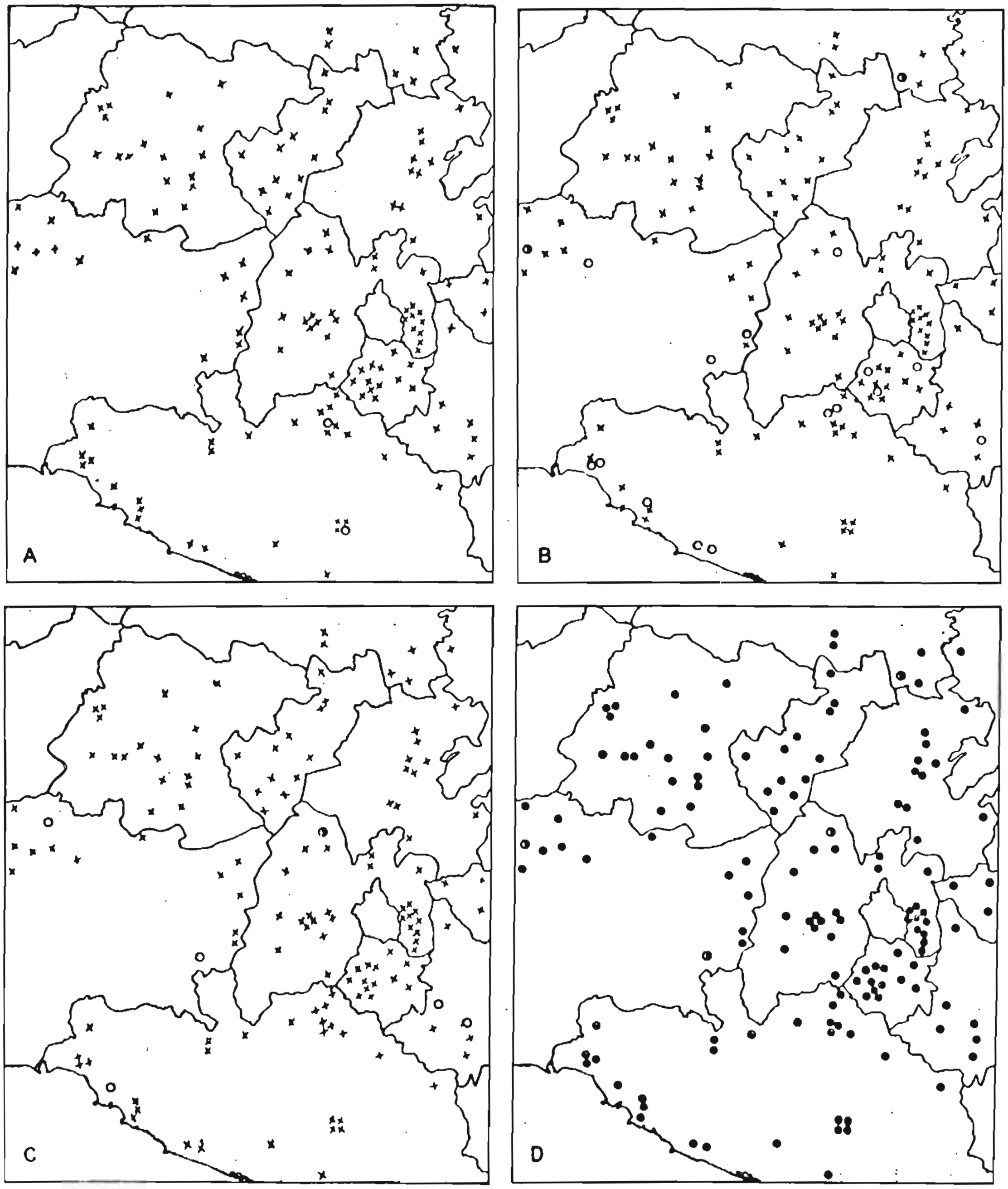

FIGURE 27. Frequency distribution of knobs at the 7S position in maize collections from central Mexico.

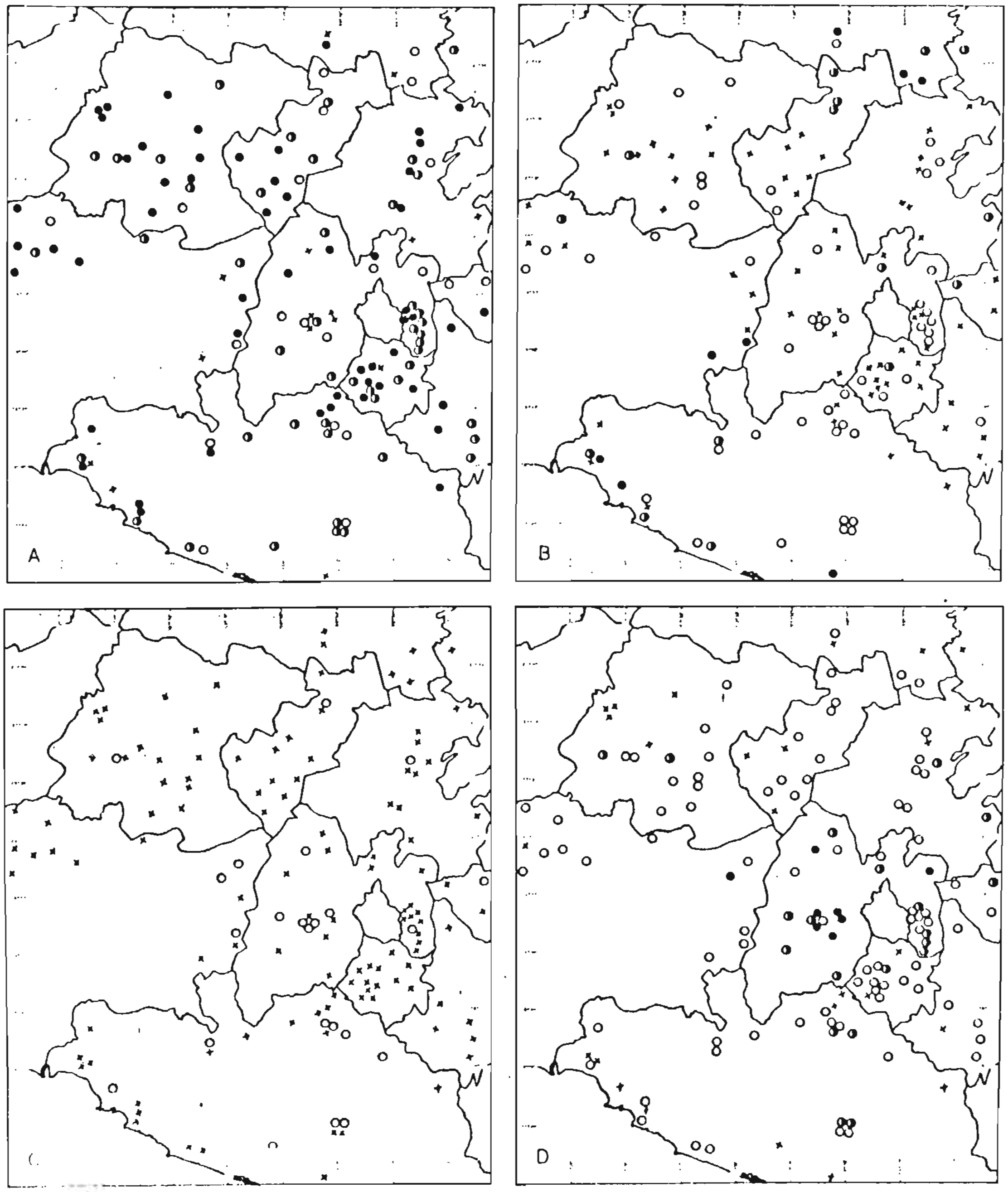

FIGURE 28. Frequency distribution of knobs at the $7L_1$ position in maize collections from central Mexico.

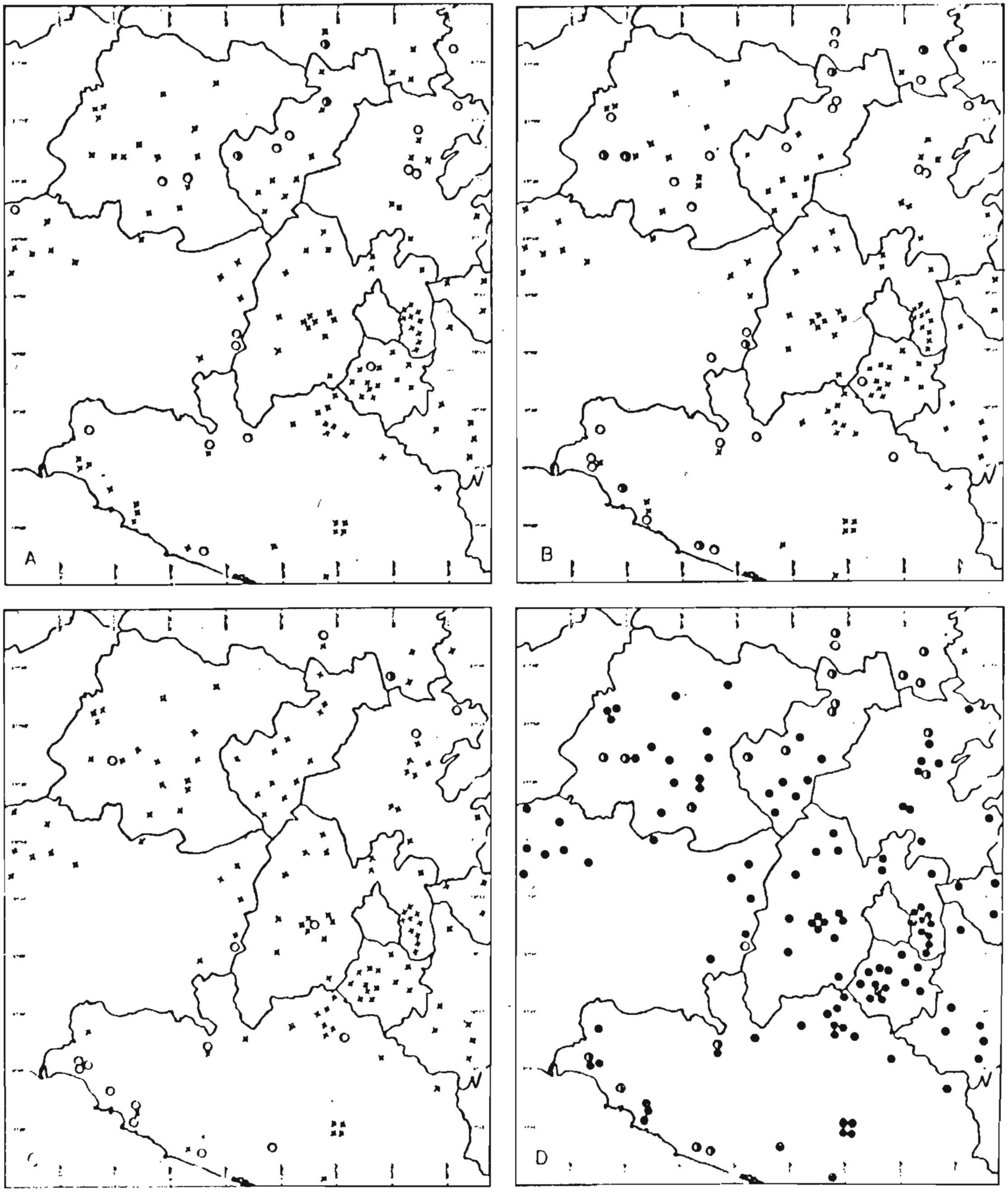

FIGURE 29. Frequency distribution of knobs at the $9L_2$ position in maize collections from central Mexico.

FIGURES 30 to 39. Geographical distribution of the relative frequencies of the several knob sizes [large, medium, small and knobless] found at different knob positions in collections of Guatemalan teosinte.

In each figure, the maps illustrate the distribution of: A. large knobs; B. medium knobs; C. small knobs; and D. knobless. Each circle represents a single collection. Black circles represent high frequencies [more than 2/3 of the total number of chromosomes of each collection]; half circles represent intermediate frequencies [1/3 to 2/3 of the total chromosomes]; open circles represent low frequencies [less than 1/3 of the total chromosomes]; and the X's represent absence of the particular knob condition that the specific map is considering.

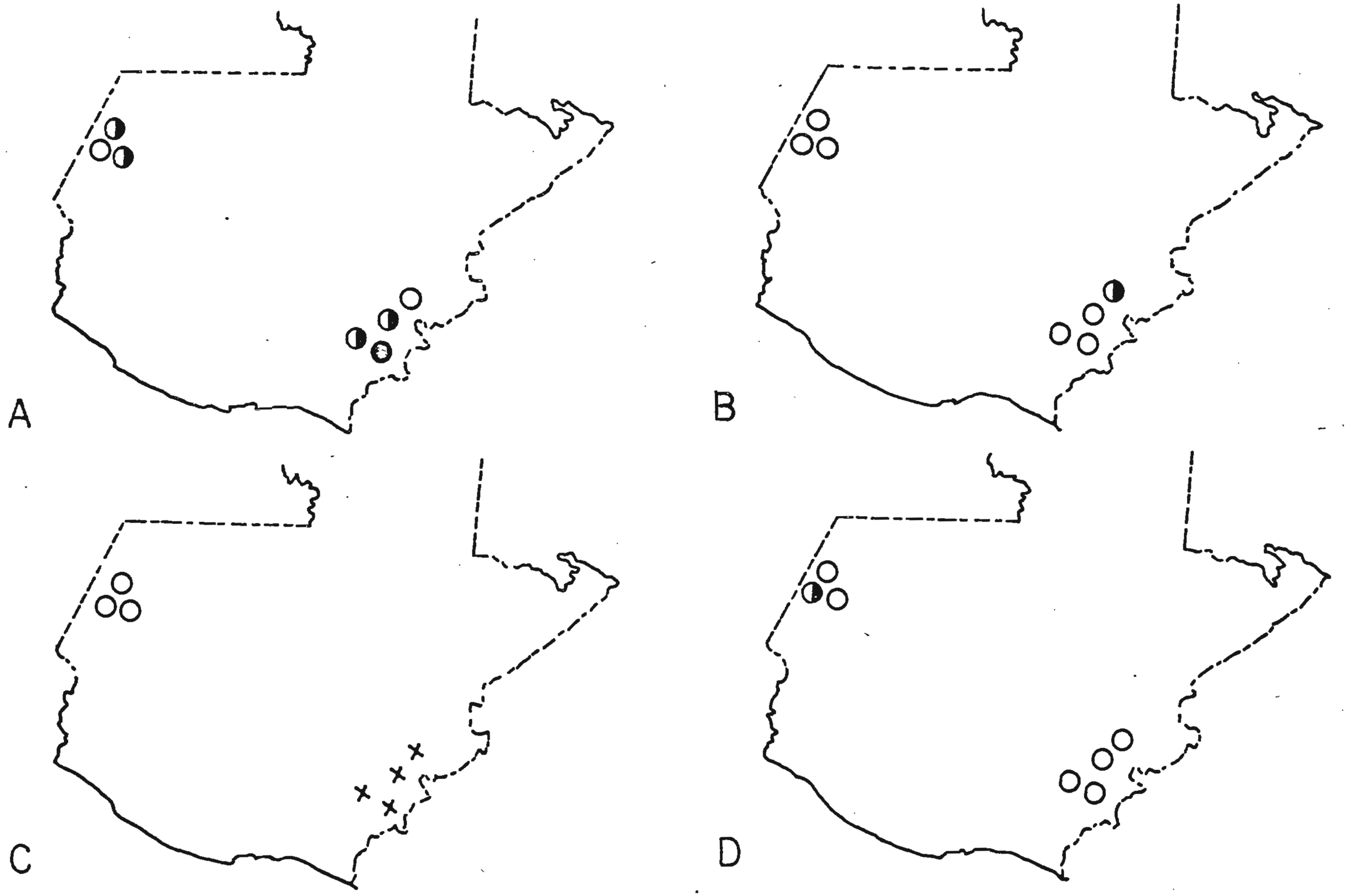

FIGURE 30. Frequency distribution of knobs at the $2S_3$ position in teosinte collections from Guatemala.

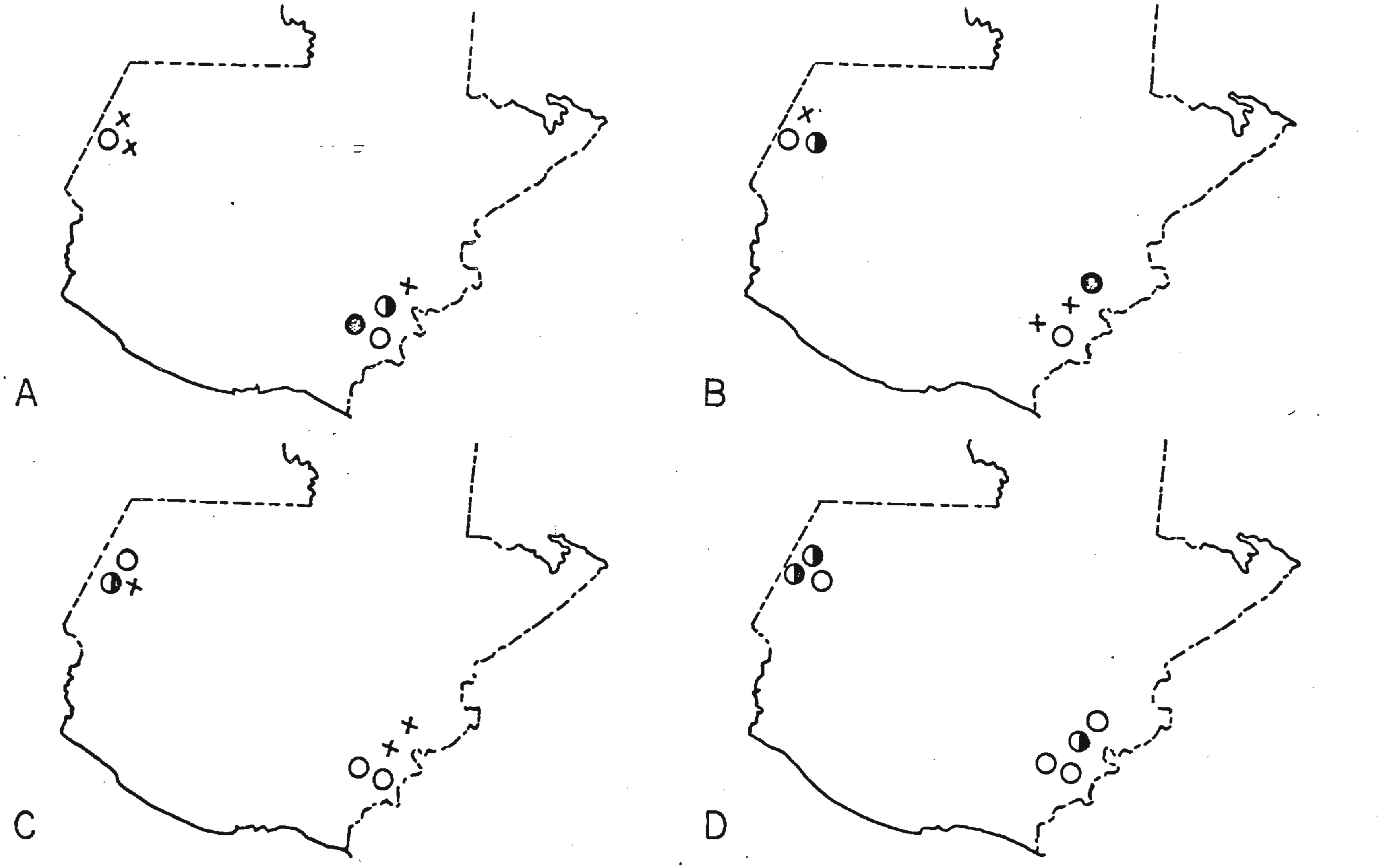

FIGURE 31. Frequency distribution of knobs at the $2L_2$ position in teosinte collections from Guatemala.

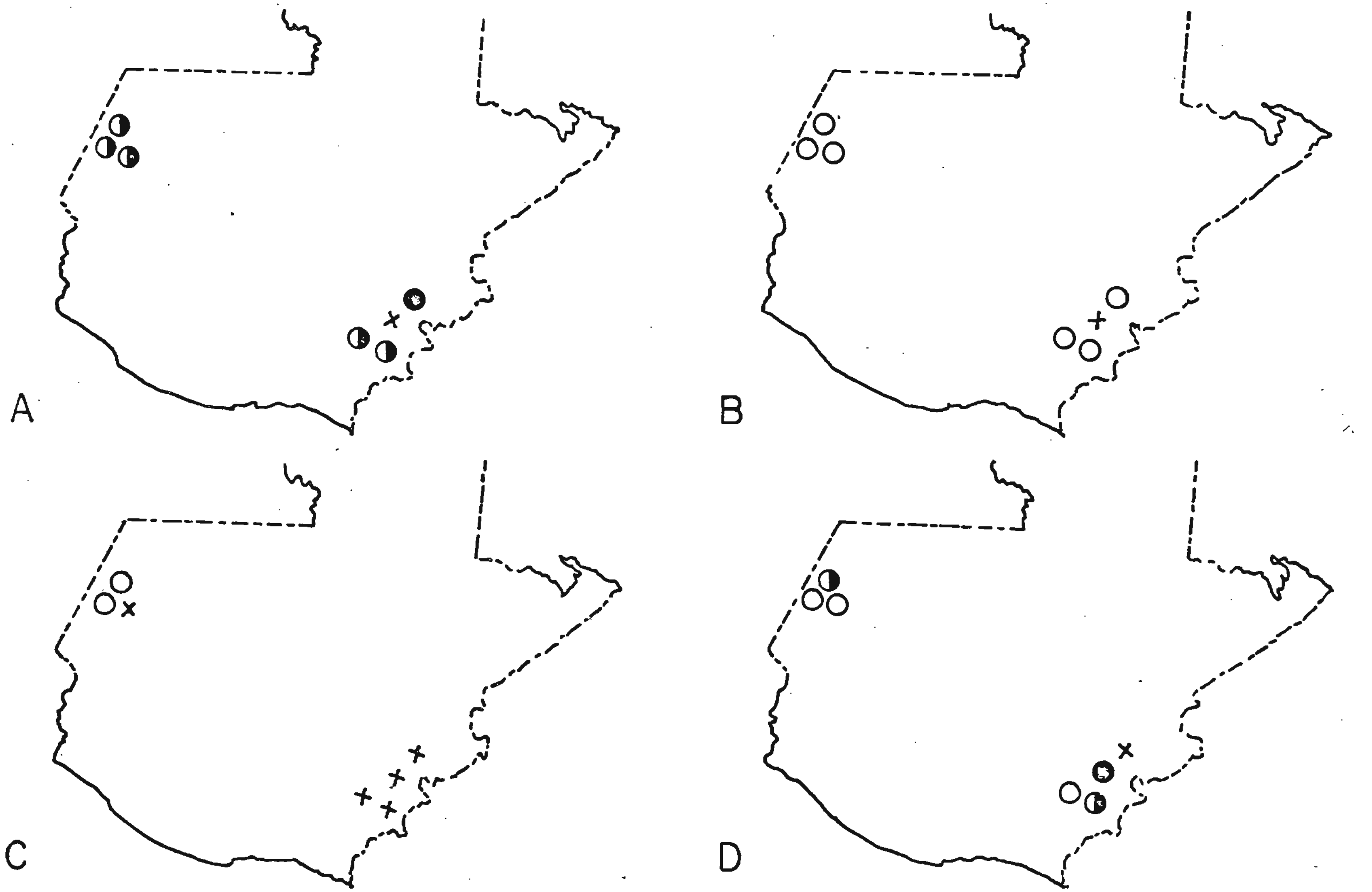

FIGURE 32. Frequency distribution of knobs at the $3S_2$ position in teosinte collections from Guatemala.

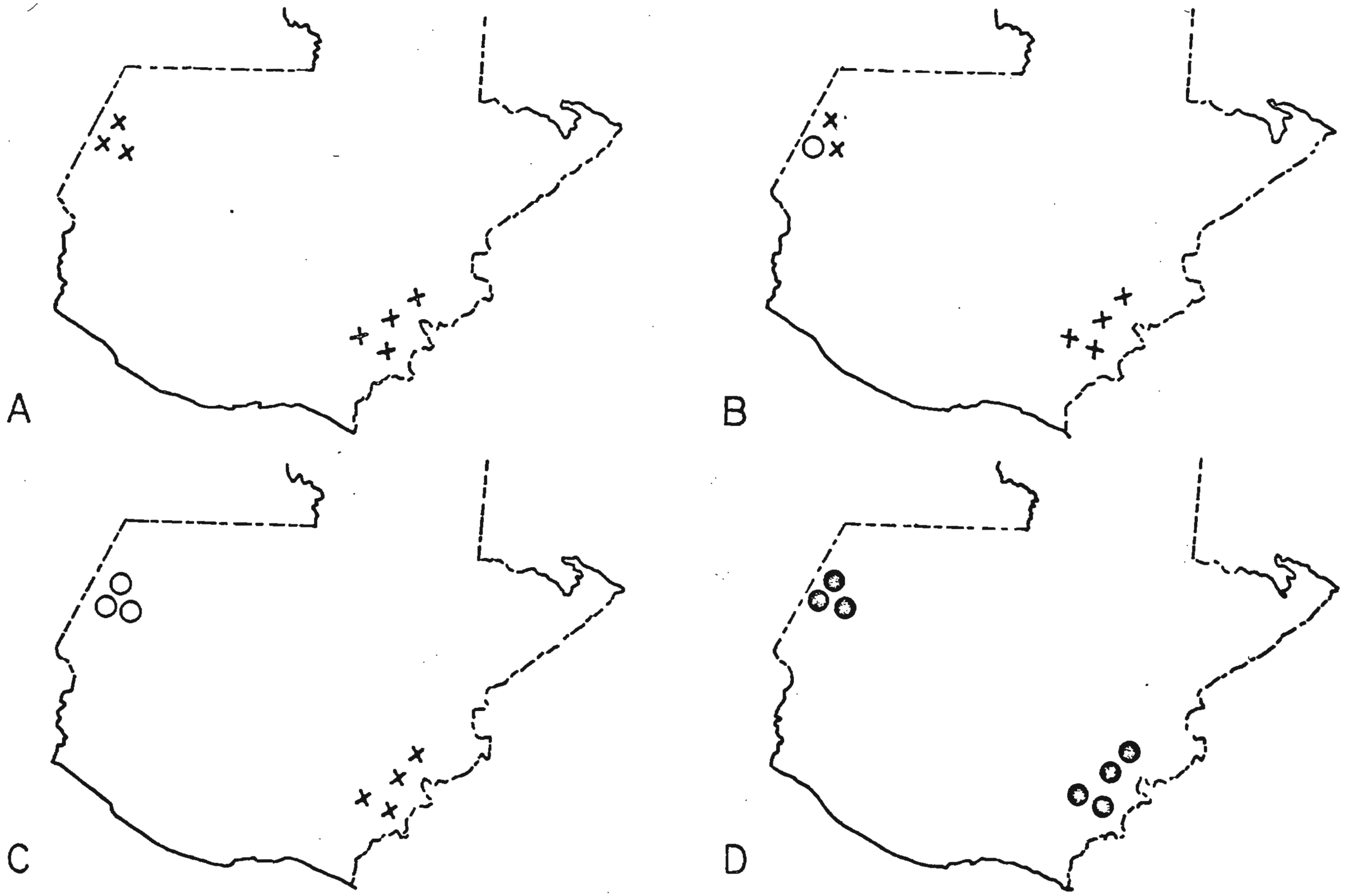

FIGURE 33. Frequency distribution of knobs at the $3L_3$ position in teosinte collections from Guatemala.

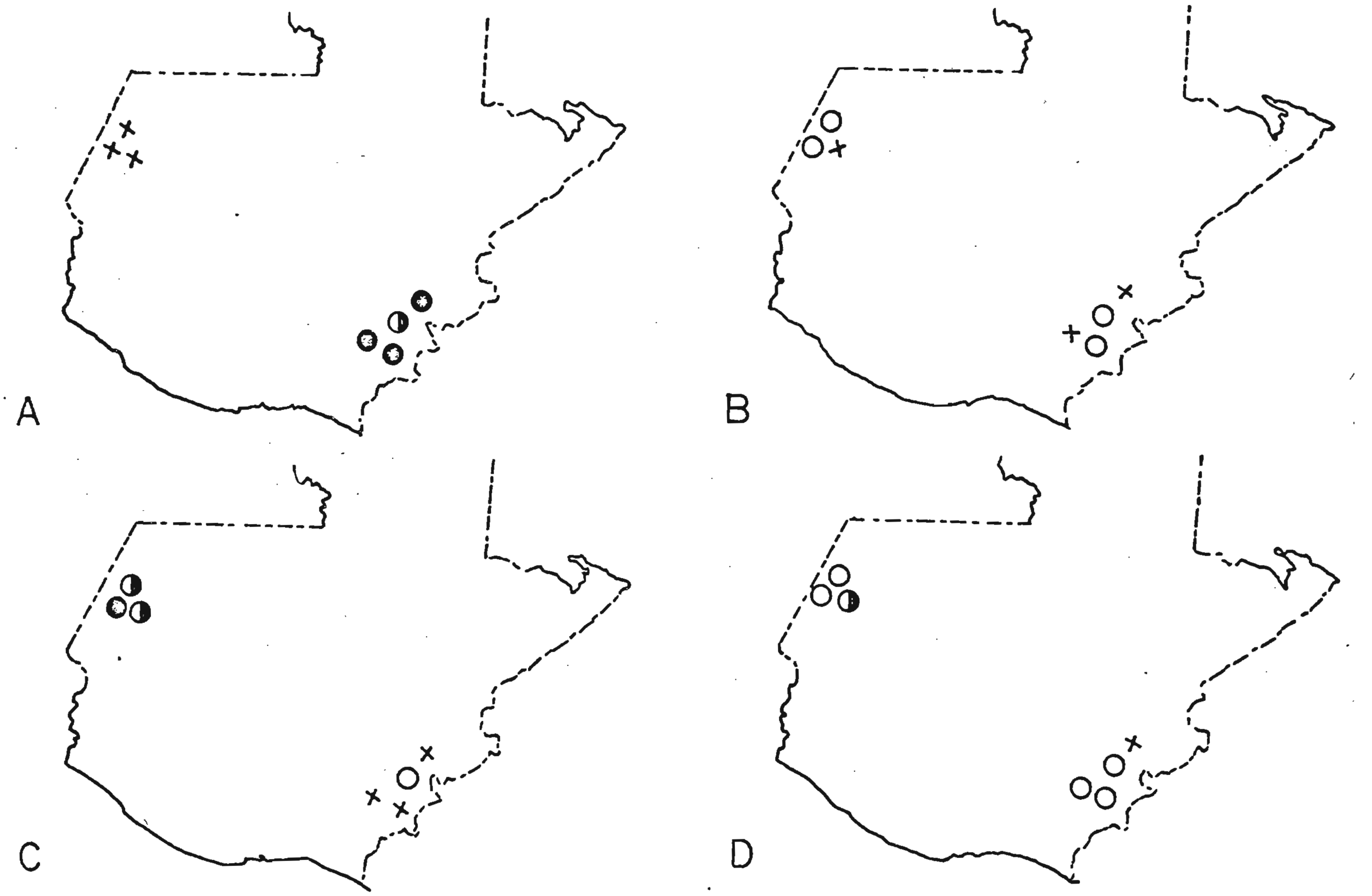

FIGURE 34. Frequency distribution of knobs at the $4S_2$ position in teosinte collections from Guatemala.

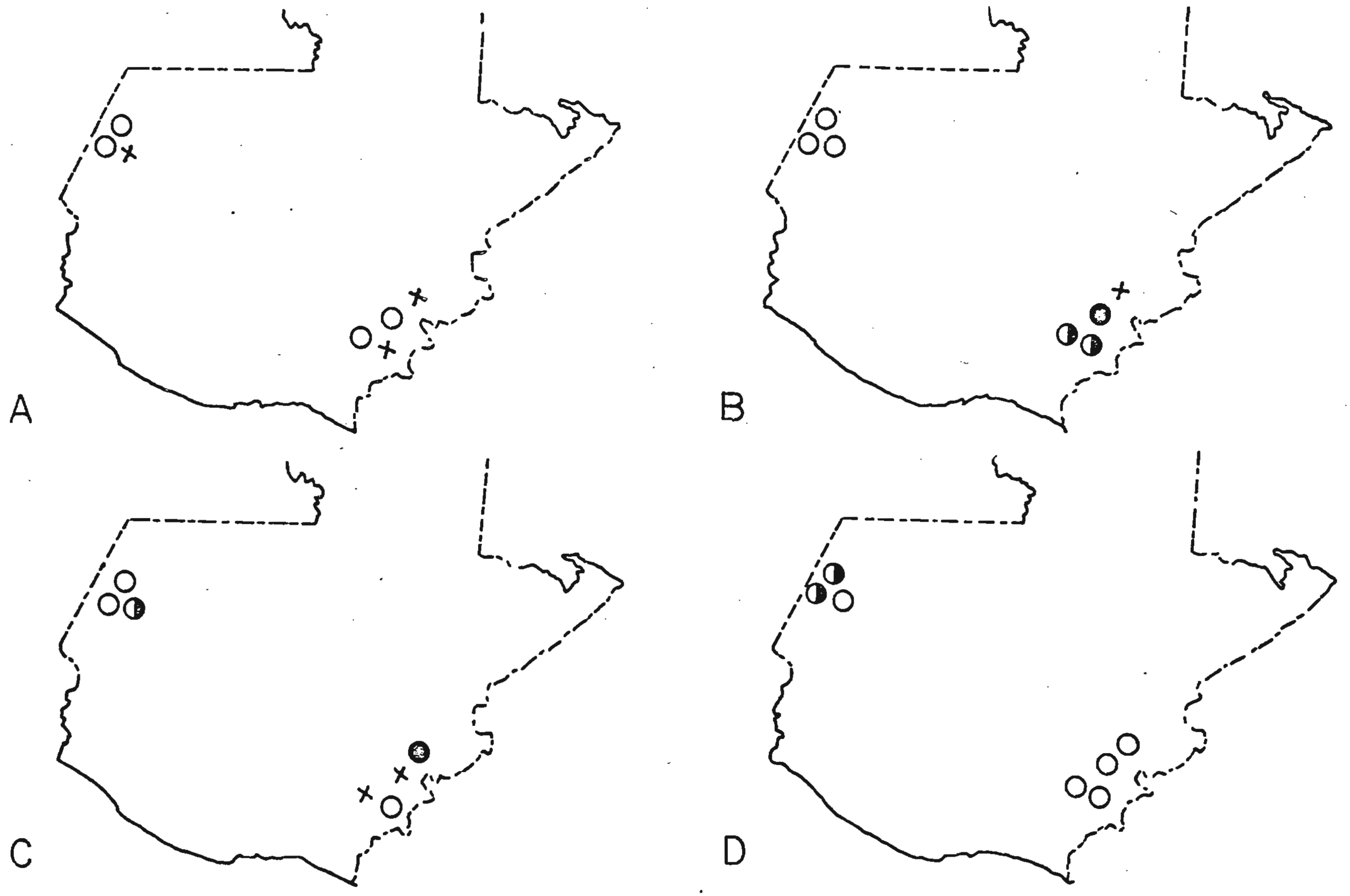

FIGURE 35. Frequency distribution of knobs at the $4L_3$ position in teosinte collections from Guatemala.

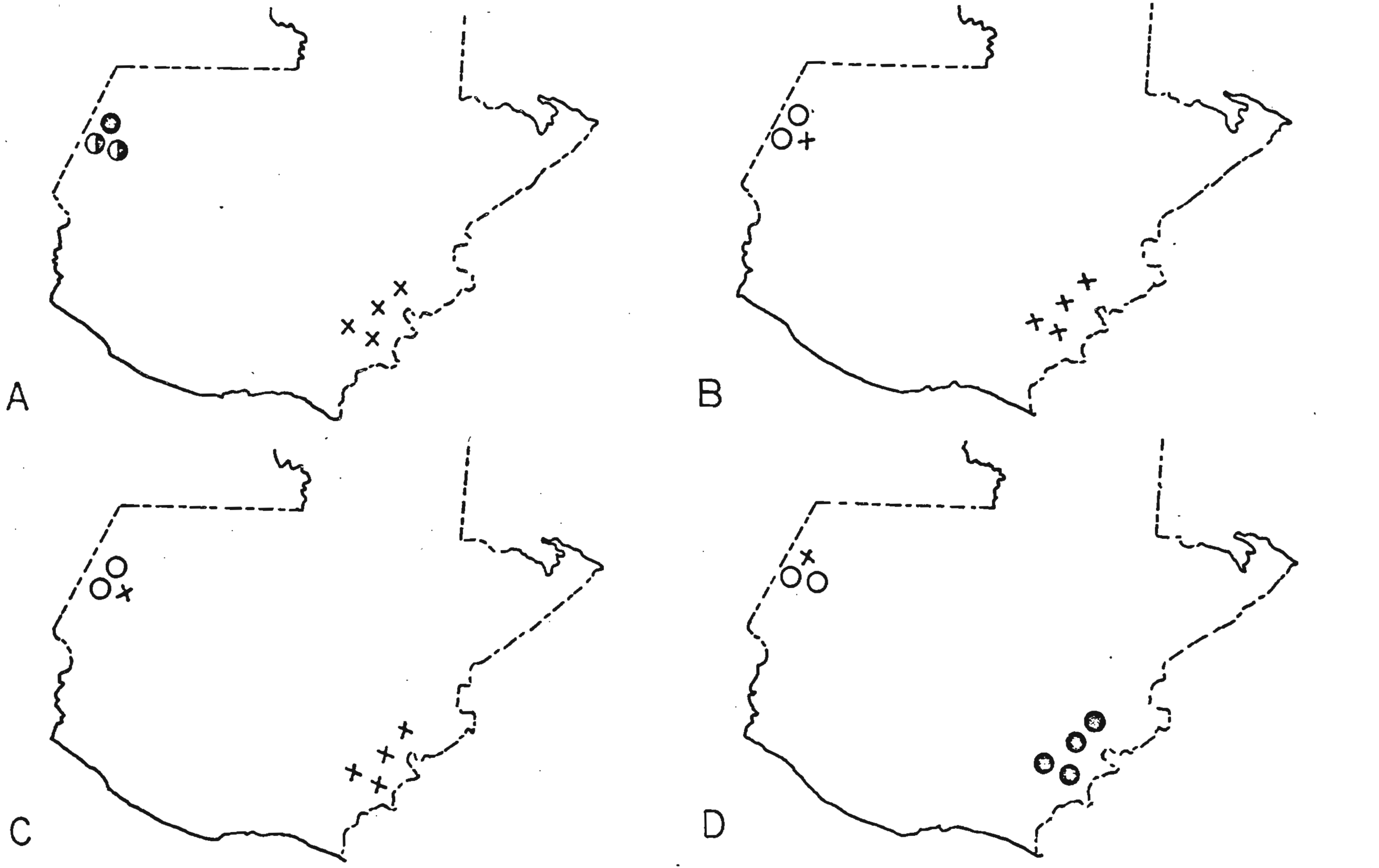

FIGURE 36. Frequency distribution of knobs at the 8S position in teosinte collections from Guatemala.

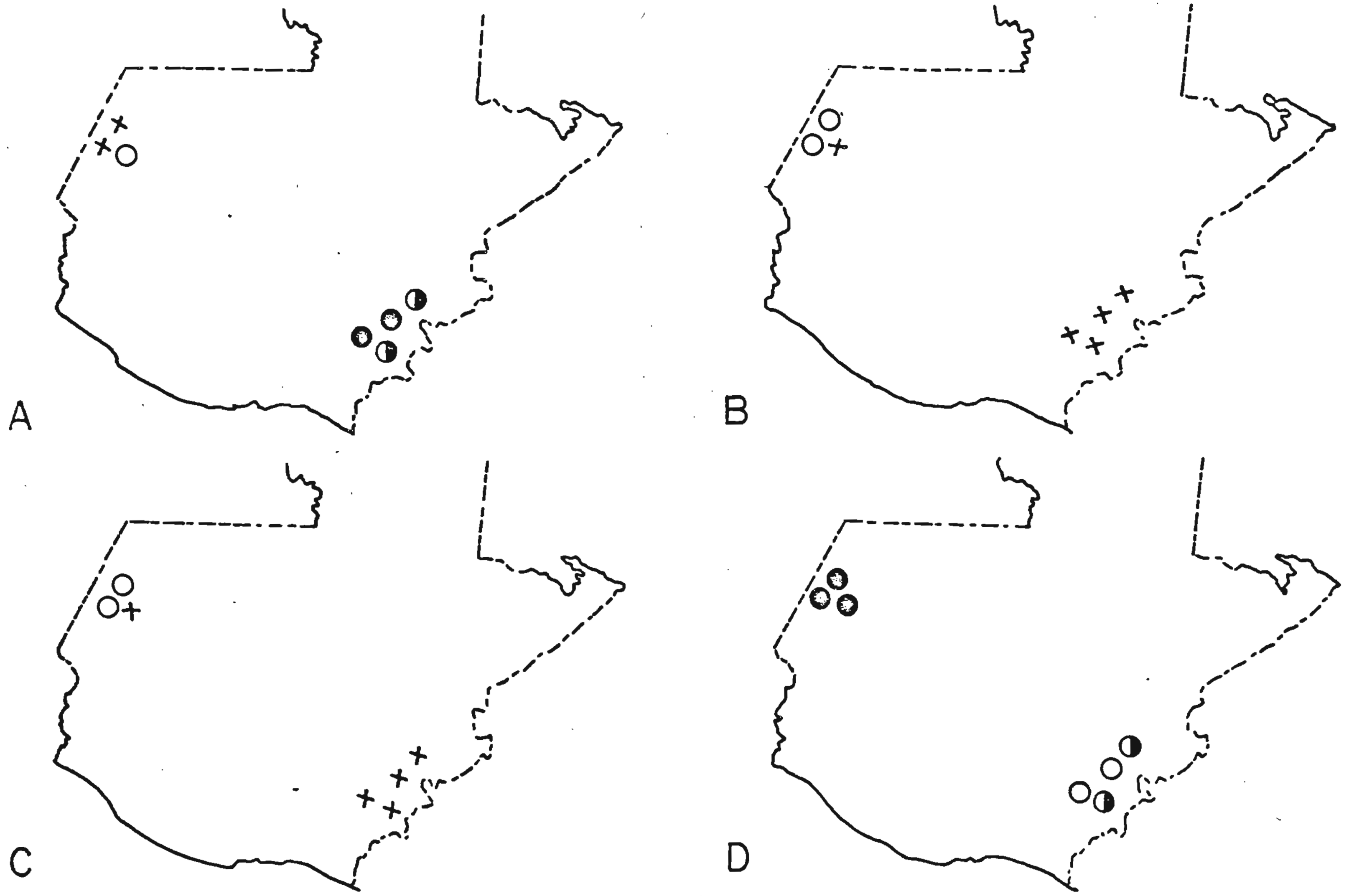

TABLE 37. Frequency distribution of knobs at the $8L_3$ position in teosinte collections from Guatemala.

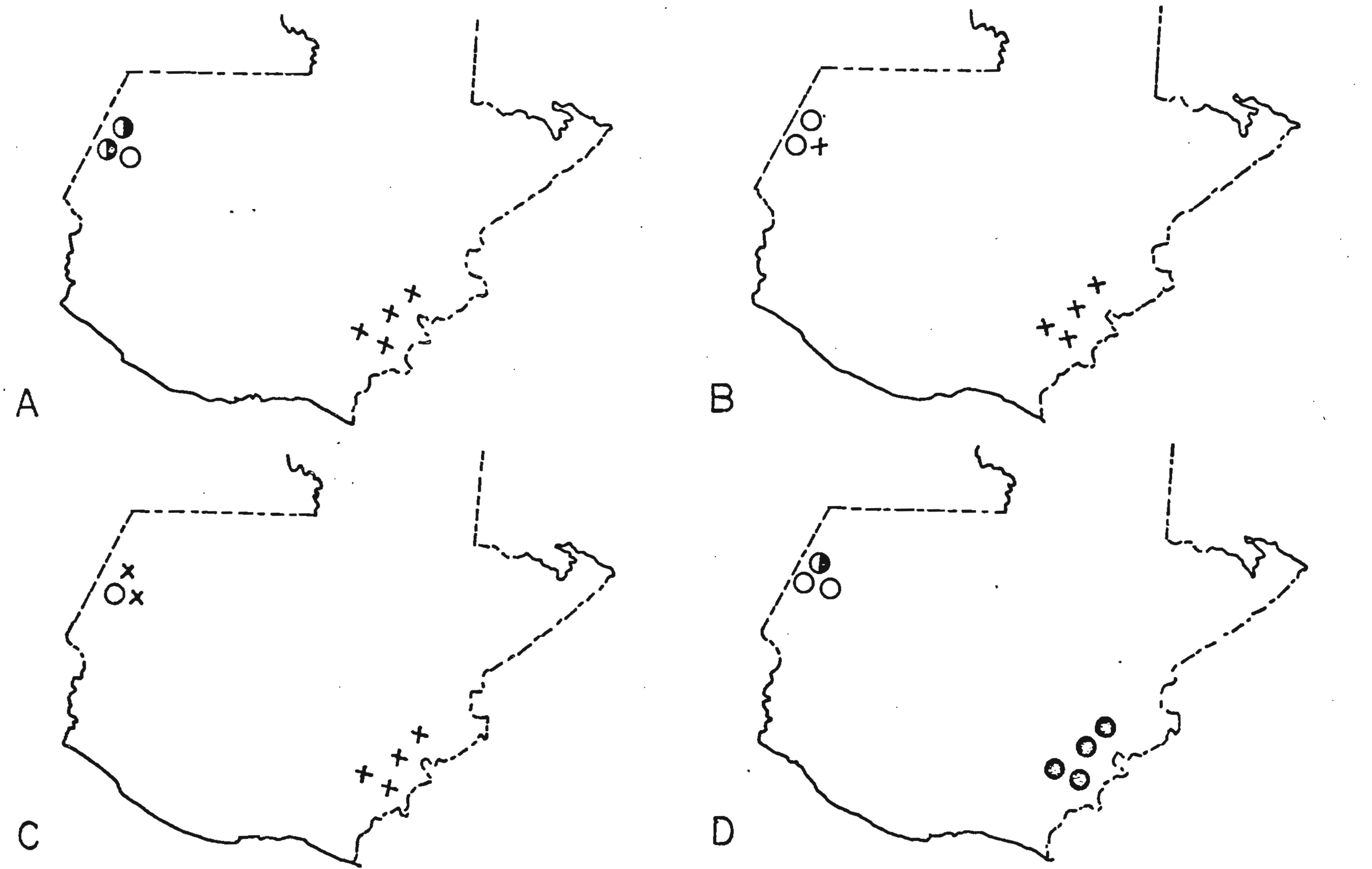

FIGURE 38. Frequency distribution of knobs at the 9S position in teosinte collections from Guatemala.

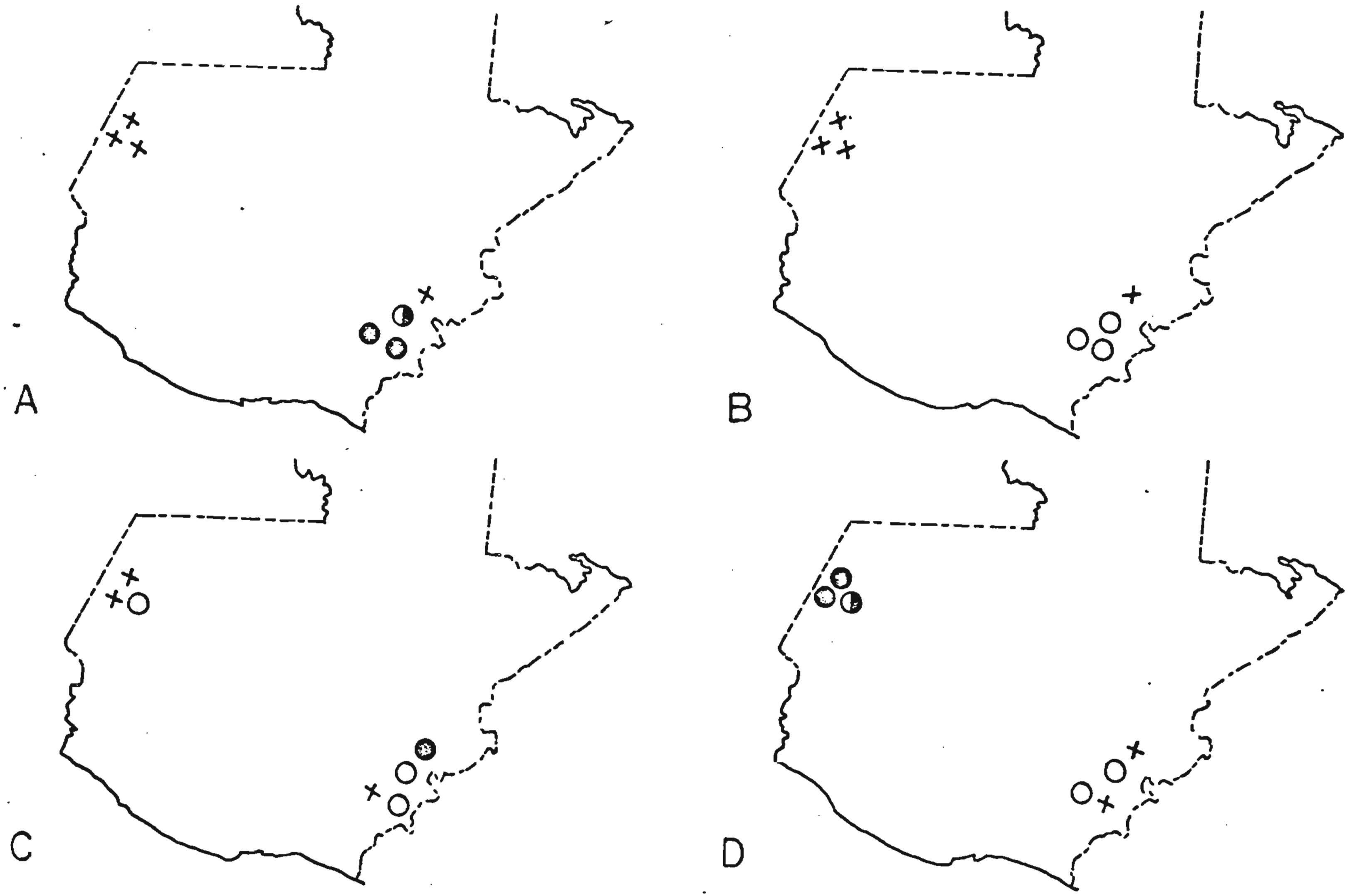

FIGURE 39. Frequency distribution of knobs at the $9L_3$ position in teosinte collections from Guatemala.

PLATE I. Pachytene chromosomes of maize and teosinte.

Figures 1 and 2. Chromosomes 1 of maize from Guerrero, Mexico and of teosinte from Huehuetenango, Guatemala. The knob is on the short arm.

Figures 3, 4 and 5. Chromosome 2 of maize from Jalisco, Mexico and of teosinte from Jutiapa, Guatemala and from the Chalco region in Mexico, respectively. Notice the similarity of the dark distal end of the long arms [arrows].

Figures 6 and 7. Chromosome 3 of maize from Yucatán, Mexico and from Huehuetenango, Guatemala, respectively.

Figures 8, 9 and 10. Chromosome 4 of maize from Sonora, Mexico and of teosinte from Huehuetenango and Jutiapa in Guatemala, respectively. The darker segments on the long arm are clearly shown [arrows].

PLATE I


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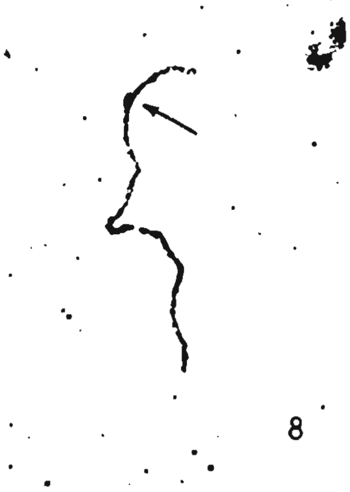
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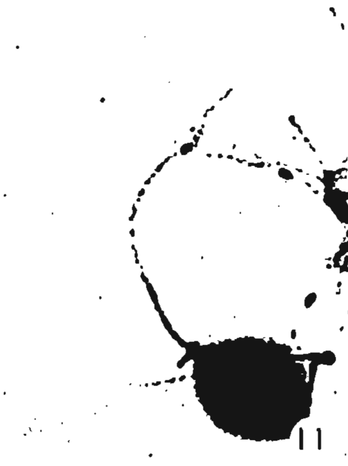
PLATE II. Pachytene chromosomes of maize and teosinte.

Figures 11, 12 and 13. Chromosome 6 of maize from Jalisco, Mexico and of teosinte from Guerrero, Mexico and from Jutiapa in southern Guatemala.

Figures 14, 15, 16 and 17. Chromosome 7 of Mexican teosinte from the Chalco region, of maize from Sonora, Mexico and of Guatemalan teosinte from Huehuetenango and Jutiapa, respectively. Notice the characteristic dark heterochromatic segment on the long arm side adjacent to the centromere [arrows].

Figures 18, 19, 20 and 21. Chromosome 8 of Mexican teosinte from the Chalco region, of maize from Jalisco, Mexico and of teosinte from Huehuetenango and Jutiapa in Guatemala.

PLATE II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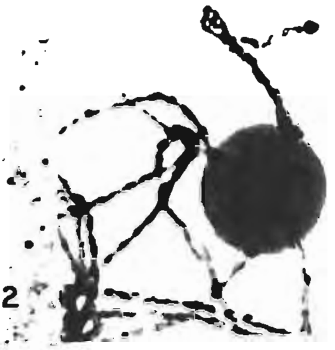
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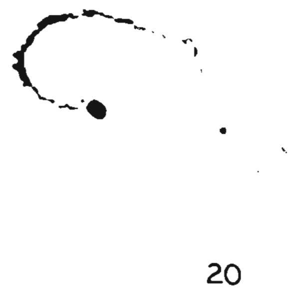
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PLATE III. Pachytene chromosomes of maize and teosinte.

Figures 22, 23 and 24. Chromosome 9 of maize from Sonora, Mexico and of teosinte from the Chalco region and Huehuetenango in northern Guatemala, respectively.

Figures 25, 26, 27 and 28. Chromosome 10 of maize from Jalisco, Mexico and of teosinte from the Chalco region and from Huehuetenango and Jutiapa in Guatemala, respectively. Notice the dark heterochromatic segment on the short arm adjacent to the centromere [short arrows] and a series of darker chromomeres on the central part of the long arm [long arrows].

Figure 29. The type II abnormal chromosome 10 found in a teosinte plant from Guanajuato, Mexico.

PLATE III

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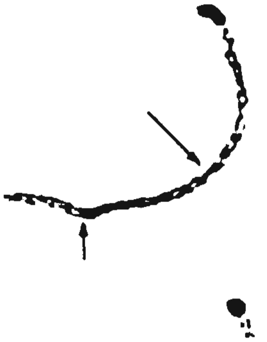

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PLATE IV. Inversions in teosinte.

Figures 30 and 31. Loops of the In8S in the hybrid Burnham's Spreader x Nobogame teosinte.

Figure 32. Loops of In8S [a] and In9S [b] in the hybrid Burnham's Spreader x Nobogame teosinte.

Figure 33. Loop of the In9S in Chalco teosinte showing that the non-inverted short arm of chromosome 9 is also present in the population.

Figure 34. Loop of the In7L in the Burnham's Spreader x Nobogame teosinte hybrid. The large knob was carried into the hybrid by the maize chromosome.

Figure 35. Loop of the heterozygous In1La in the Burnham's Spreader x Nobogame teosinte hybrid. The small knob is located within the inverted segment.

Figures 36 and 37. Loops of the heterozygous In1Lb found in the Burnham's Spreader x Northern Guatemala teosinte F_1 hybrid. Notice that the loops are larger than the one of In1La of Figure 35.

PLATE IV

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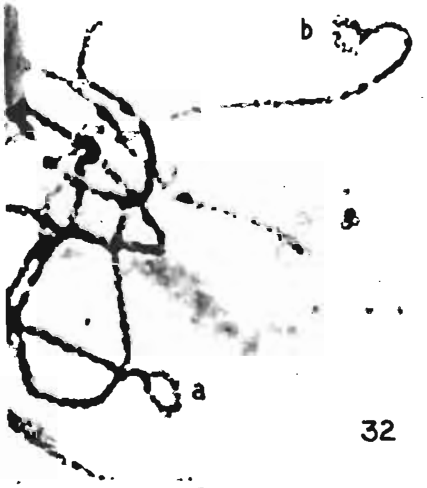

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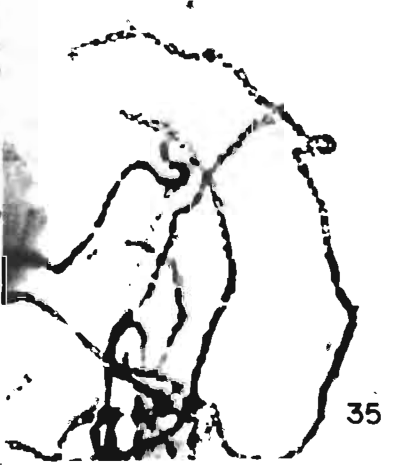

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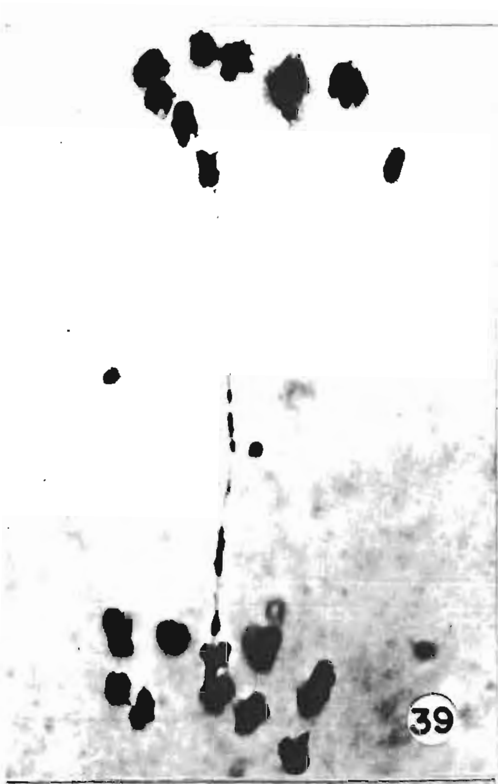
PLATE V. **Bridges and fragments at anaphase I in maize** x teosinte hybrids.

Figure 39, 40 and 41. Single bridge and single fragment configurations at anaphase I due to crossing over in heterozygous inversions found in a Burnham's Spreader x Nobogame teosinte hybrid.

Figure 42. Two bridges and two fragments due to crossing over in two independent heterozygous inversions in a Burnham's Spreader x Nobogame teosinte hybrid. Notice differences in the fragment sizes compared to those of Figures 39, 40 and 41.

PLATE V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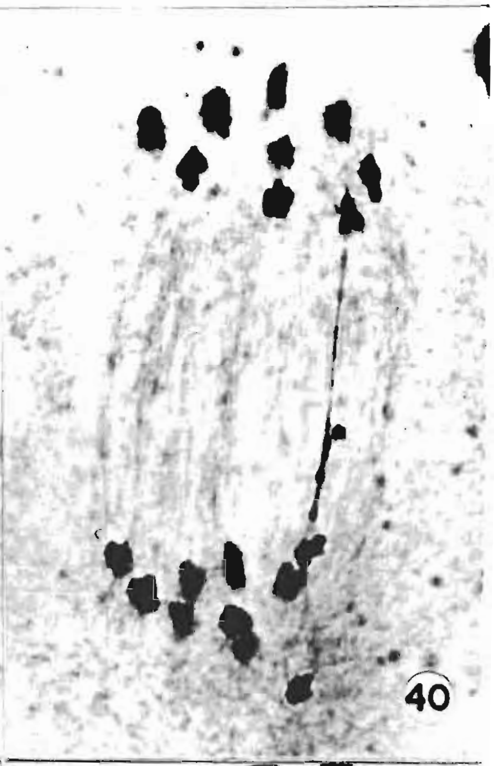
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PLATE VI. Pairing irregularities at pachytene and inversion loops in maize x teosinte hybrids. Also different pollen abortion due to inversions and irregular pairing in maize x teosinte hybrids.

Figure 43. Non-pairing of the region with the heterozygous inverted segment in the long arm of chromosome 7 [In7L] in a maize x Nobogame teosinte hybrid.

Figure 44. Non-pairing of the distal segment adjacent to the knob on the long arm of chromosome 4 in the hybrid between maize and Northern Guatemala teosinte.

Figure 45. Non-pairing of a large segment about the knob on the long arm of chromosome 2 in a hybrid between maize and Guerrero teosinte.

Figures 46 and 47. Loop configuration of the heterozygous In9S found in the maize x Southern Guatemala teosinte. Notice the poor spreading of the chromosomes.

Figure 48. Non-pairing of a complete chromosome. One of the univalents is shown at the lower right of the picture. The other homologous chromosome should be somewhere within the clumped chromosomes.

Figure 49. Normal pollen fertility shown by the maize x Nobogame teosinte hybrid. Actually few grains are aborted due to the presence of heterozygous inversions and other unknown factors.

Figure 50. Pollen abortion in the maize x Jutiapa teosinte hybrid.

Figure 51. Pollen abortion in the hybrid between teosinte from Chiquimula in Southern Guatemala and Guerrero in Mexico. Notice that the degree of pollen abortion is similar but the grain size is more variable than the case shown in Figure 50. The high pollen abortion rate is the consequence of a high degree of asynapsis during the meiotic prophase and further irregular segregation of the chromosomes at anaphase I illustrated in Figure 48 of Plate VI, and Figures 52 to 56 in Plate VII.

PLATE VI


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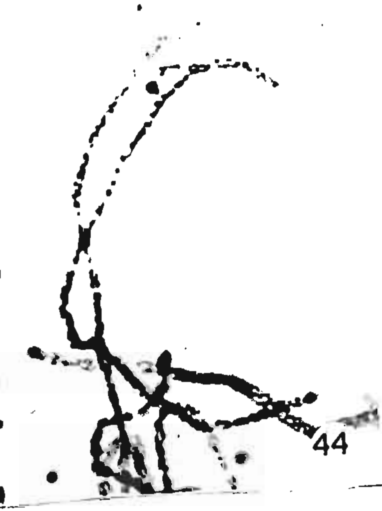
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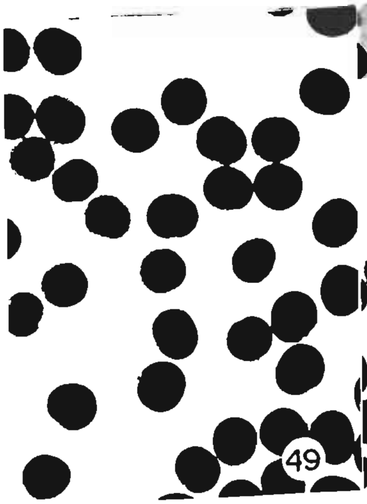
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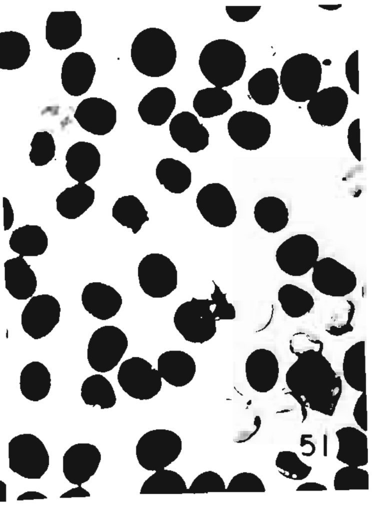
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PLATE VII. Irregular pairing and segregation at meiosis in a maize x Southern Guatemala teosinte hybrid.

Figure 52. 7 II + 6 I at diakinesis.

Figure 53. 9 II + 2 I at metaphase I.

Figure 54. 8 II + 4 I at metaphase I.

Figure 55. 6 II + 8 I at metaphase I.

Figure 56. 12 - 8 segregation at anaphase I.

PLATE VII

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